University of Alberta

Management and Ecology of Alpine Lakes

by

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ABSTRACT

The 1960s stocking of non-native Brook Trout (*Salvelinus fontinalis*) into fishless alpine Bighorn Lake led to the loss of the large crustaceans *Hesperodiaptomus* and *Daphnia*, leaving the lake dominated by small cyclopoid copepods and rotifers. Following gillnet removal of Brook Trout in the 1990s, *Daphnia* returned to pelagic waters. *Hesperodiaptomus* did not return, due to exhaustion of its resting egg bank. *Diacyclops* and rotifer abundance remained high in the absence of *Hesperodiaptomus*. Beginning three years after fish removal began, phytoplankton biomass fell 70-fold relative to reference Pipit Lake. All phytoplankton taxa except for cyanophytes exhibited decreased biomass. Chlorophyll-*a* concentration was unresponsive to fish manipulation. Secchi disc depth increased from 3.5 m to maximum lake depth (9.2 m), probably as a result of zooplankton filtering of inorganic sediments from lake-water. No changes in nutrient concentrations in lake water were attributable to fish manipulation.

Reduction of angling mortality of Bull Trout (*S. confluentus*) on two small lakes had variable effect on Bull Trout abundance. Bull Trout abundance increased ~5-fold for Harrison Lake and was associated with reduced individual growth rates. Size-based competitive asymmetries between Bull Trout born before and after reduction in angling mortality led to the loss of at least 15 year-classes of large, old Bull Trout. For Osprey Lake, closure of the lake to angling did not increase Bull Trout abundance. One or more of illegal angling, trophic restructuring of the population and high immigration rate probably limited the scope for population abundance responses at this site.

A Common Loon caused strong predator avoidance responses in pelagic adult Bull Trout in Harrison Lake. Size segregation of adult and juvenile Bull Trout was lost

when adults occupied littoral predation refuges and cannibalism of juveniles by adults increased. Food consumption of adult Bull Trout increased in the presence of a loon, as a result of increased cannibalism, but decreased for juveniles. Low juvenile food consumption was correlated with low growth rates. Daily juvenile biomass losses due to loon-induced cannibalism were similar to probable losses due to direct predation by loons.

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CHAPTER ONE: GENERAL INTRODUCTION

INTRODUCTION

Early high-elevation lake management in the national parks

Beginning with the creation of the mountain national parks of Canada and the United States of America (US) as tourist destinations between the mid-late 1800s and the early 1900s, and continuing through the mid-late 1900s, parks management primarily was directed towards providing recreational opportunities for parks visitors (Franke 1996; Schindler 2000). Sportfishing was a particularly important and heavily promoted recreational activity (Vick 1913; Rawson 1940; Solman 1950a; Dominion Bureau of Statistics 1956; Nicola 1976; Franke 1996). Salmonid populations near tourist centres were heavily exploited by the early 1900s and the supplemental stocking of both native and non-native fish species was initiated between 1890 (US) and 1901 (Canada) to maintain high catch rates for tourists (Vick 1913; Donald 1987; Franke 1996). Following the development of techniques to transport fish by horse-pack in the 1920s (Donald and Alger 1986) many remote lakes and streams were stocked to increase the number and variety of fisheries available to anglers (Ward 1974; Nicola 1976). Private and illegal fish stocking also contributed to the proliferation of non-native fish populations (Drake and Naiman 2000; Ruczynski and others 2003). By the late 1970s, ~25% of Canadian mountain park lakes had been stocked (Schindler 2000). A high proportion of US mountain lakes were stocked with non-native salmonids (Bahls 1992).

Concurrent with active and expanding fisheries enhancement programs, the number of anglers fishing mountain park waters also increased (Franke 1996, 1997). Between 1950, when records of angling license sales for Canadian national parks were first formally maintained, and 1982, angling license sales increased 5-fold. Further, a combination of the development of lightweight camping gear, increased leisure time and improved access ensured that even remote lakes were accessible to anglers.

The effects of lake management on native aquatic biota

Little consideration was given to the effects of fisheries enhancement activities and high angler effort on native fish stocks. Where high angler effort was combined with the introduction of Brook Trout (*Salvelinus fontinalis*) or Lake Trout (*S. namaycush*) or their hybrid Splake, some native Bull Trout populations were extirpated (Donald and Alger 1993; Donald and Stelfox 1997). Native Cutthroat Trout (*Oncorhynchus clarkii*) were replaced by or hybridized with introduced Rainbow Trout (*O. mykiss*) (Nelson 1965; Franke 1996; Kruse and others 2000) or partially or wholly replaced by Brook Trout (Dunham and others 2002). Losses of native salmonids continue through to the present as non-native fishes expand their distributions following their initial introductions (Fredenberg 2002; Paul and others 2003).

Comparatively little information is available on the effect of high angler effort and angling mortality on native fish stocks that were not 'enhanced' through stocking. Survey work on mountain park fish populations was limited and generally consisted only of creel surveys (Solman 1950b) and/or a few days of gillnet fishing (Dominion Bureau of Statistics 1956; also see for example Anderson and Donald 1978; Donald and DeHenau 1981), the latter often conducted years or decades after sport fishing was initiated.

Stocked non-native fishes had significant impacts on many originally fishless waterbodies. Native amphibians were reduced in abundance or locally extirpated (Bradford 1989; Tyler and others 1998; Bull and Marx 2002; Knapp and others 2002). Large aquatic invertebrate species, including *Gammarus*, *Daphnia* and the keystone species *Hesperodiaptomus* often were eliminated (Anderson 1972; Anderson and Donald 1978; Anderson 1980; Stoddard 1987; Bradford and others 1998; Liss and others 1998; Donald and others 1994; McNaught and others 1999; Donald and others 2001; Knapp and others 2001; Schindler and Parker 2002; Sarnelle and Knapp 2004). Rotifers flourished in the absence of predatory calanoid copepods (Anderson 1977; Anderson 1980; Paul and Schindler 1994; Knapp and others 2001). Large algal species replaced smaller species (McNaught and others 1999), shifts in diatom composition occurred (Drake and Naiman 2000) and strong cascading trophic interactions leading to high phytoplankton biomass were inferred to have occurred (Leavitt and others 1994; Schindler and others 2001) in some lakes. Similar results have been reported from studies of fish introductions in originally fishless high elevation lakes in other regions (Nilsson 1972; Pechlaner 1984; Gliwicz 1990; Braña and others 1996). Non-native fish introductions also impacted terrestrial habitats via the elimination or reduced abundance of aquatic prey species important to terrestrial predators (Matthews and others 2002; Ruzycki and others 2003).

Recent lake management in the national parks

Changes in management directive that elevated the maintenance of ecological integrity and the restoration of damaged ecosystems to the highest priority of national park managers were formally enacted in 1988 in Canada and after 1963 in the USA (Nicola 1976; Franke 1997). As a result, the stocking of non-native fishes was terminated and increasingly restrictive angling regulations for native fish species were imposed. In the absence of continued stocking, non-reproducing populations of stocked fish collapsed, while reproducing populations persisted in numerous lakes where suitable spawning habitat was available (Donald 1987; Armstrong and Knapp 2004; Sarnelle and Knapp 2004). Cessation of fisheries enhancement activities and regulatory changes were coincident with a reduction in the number of anglers fishing both US (Franke 1997) and Canadian mountain parks.

The effects of new management regimes on native aquatic biota

The reduction in the intensity of fisheries enhancement activities and human use created a series of whole-lake ecosystem manipulations. Parker and others (1996), Funk and Dunlap (1999), Knapp and Matthews (2000), Donald and others (2001), Knapp and others (2001), Schindler and Parker (2002) and Vredenburg (2004) exploited these whole-lake manipulations as tests of the resistance and resilience of high-elevation, originally fishless lakes to biotic perturbation. Their studies document low ecosystem resistance to fish stocking, particularly in smaller, shallower lakes (Donald and others 1994) and low to high resilience depending on lake elevation and the duration of the perturbation. If elevations were low or stocked fish populations persisted for comparatively short periods, recovery of pre-stocking aquatic communities to near pristine condition generally occurred within 1-3 decades (Parker and others 1996; Knapp and others 2001; Schindler and Parker 2002). However, high-elevation aquatic

ecosystems were not as resilient to the prolonged presence of fish (Parker and others 1996; Knapp and others 2001; Schindler and Parker 2002). In originally fishless lakes, large *Hesperodiaptomus* species failed to recover in some stocked lakes even if fish eventually were eliminated. Limited persistence of diapausing egg banks was responsible (Parker and others 1996; Knapp and others 2001). In some cases, algal communities failed to recover even 2-3 decades after stocked fish were lost (Drake and Naiman 2000). Where non-native salmonids persisted, no ecosystem recovery occurred and populations of co-occurring native fishes, if present, and invertebrates remain either extirpated or at abundance levels uncharacteristic of never-stocked lakes (Knapp and others 2001; Schindler and Parker 2002).

Little is known about the resilience of native fish populations in never-stocked lakes in the face of reduced angling mortality on native fish populations. Reductions in fishing mortality led to increased native fish abundance and changes in individual growth rates and population structure in some watersheds (Herman 1997; Mushens and others 2001), but whether such responses are common over large geographic areas is unknown.

RESEARCH OBJECTIVES

Two research opportunities associated with whole-lake management manipulations have remained unexplored in lakes of the Canadian mountain national parks. First, for lakes where populations of non-native salmonids have persisted, and thus no aquatic ecosystem recovery occurred, the restoration of pristine pre-stocking food webs by non-native salmonid removal has never been attempted. Removal of native *Catostomus* species and angler-introduced cyprinids, using fish toxicants, was attempted on nearly two-dozen occasions, but generally was not successful. Limited experimental fish removal of stocked salmonids began in the western US in the late 1990s (Knapp and Matthews 1998; Vredenburg 2004). Second, for native fish lakes that had never been stocked there has not been a formal evaluation of the effects of reduced angling effort and angling mortality on their fish populations. The research work conducted herein addresses both of these research opportunities, from both management and ecological perspectives.

Our research objectives were fourfold:

First, to use gillnets to remove a population of self-sustaining non-native Brook Trout from originally fishless, alpine Bighorn Lake (Chapter Two). We hoped to restore the lake's aquatic invertebrate community to its pristine condition. The Banff-Bow Valley Study (1996) recommended experimental restorations of this type to determine if damaged national park resources could be restored by non-native fish removal. However, we expected incomplete recovery of the planktonic community of Bighorn Lake following Brook Trout removal because of the prolonged period of perturbation (Parker and others 1996; Knapp and others 2001) and the previous experience of McNaught and others (1999).

Second, to use the experimental removal of Brook Trout from Bighorn Lake as a test of cascading trophic interaction (CTI) theory (Carpenter and others 1985) in an oligotrophic, species-poor lake (Chapter Three). CTI generally are thought to be weak in oligotrophic ecosystems (Sarnelle 1992; Mazumder 1994; but see McQueen and others

1986) but strong in species-poor ecosystems (Power 1990; Strong 1992; Polis and others 2000). Leavitt and others (1994) had previously inferred strong pelagic CTI in nearby alpine lakes using sub-fossil pigment chronologies but no direct observations were available to support these inferences. We hypothesized that CTI should be weak because of low lake productivity.

Third, to determine if reduced angler access and angling mortality on two native Bull Trout populations, one in a remote alpine watershed and the second in a road-accessible montane lake led to increased Bull Trout abundance (Chapter Four). Bull Trout are known to highly vulnerable to angling (Sullivan 2001; Paul and others 2003; Post and others 2003) but the response of adfluvial populations to near cessation of angling has been only infrequently documented (but see Herman 1997; Mushens and others 2001). We hypothesized Bull Trout abundance would increase in both populations following a change in management regimes in the late 1980s.

Fourth, to assess the effects of piscivorous bird predation on a small isolated Bull Trout stock (Chapter Five). Because the number of fish-bearing lakes is decreasing, as stocked fish populations fail or are deliberately removed, we expected that native fish stocks would become increasingly important food resources to piscivorous diving birds and that bird predation would increase in intensity. We hypothesized that the addition of an avian predator would elicit strong behavioural responses in Bull Trout, as observed in other fish populations (Gilliam and Fraser 1987; Power 1990) and that interference interactions between juvenile and adult Bull Trout would increase. This latter work was developed as a result of observations made while conducting objective three.

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CHAPTER TWO: THE EFFECTS OF STOCKING AND REMOVAL OF A NON-NATIVE SALMONID ON THE PLANKTON OF AN ALPINE LAKE[1]

INTRODUCTION

In the early part of the 20th Century sport fish were widely stocked in high-elevation fishless lakes of the national parks of the Canadian Rocky Mountains (reviewed by Schindler and Pacas 1996; Schindler 2000). Many of the smaller stocked lakes did not have suitable spawning habitat and fish populations dwindled to extinction within a few decades after stocking ceased, in some cases leaving the invertebrate communities of the lakes impoverished (McNaught and others 1999; Parker and others 1996; Knapp and others 2001). In other alpine and subalpine lakes, introduced Brook Trout (*Salvelinus fontinalis*) spawned successfully and populations were self-maintaining, although the value of these populations to regional sport-fishing was variable (Rawson 1940; Donald and others 1980; Donald 1987). Bighorn Lake was one of the alpine lakes that supported stocked Brook Trout.

We infer from early records that introduced fish eliminated the large crustaceans *Hesperodiaptomus arcticus* and *Daphnia middendorffiana* (Figure 2.1) from the zooplankton of Bighorn Lake (Anderson 1972; Anderson and Donald 1978). When studies of the lake resumed in 1991 the zooplankton community was still in an altered state. *Hesperodiaptomus* and *Daphnia* were absent, and there were few crustaceans observed in the plankton. In nearby fishless Snowflake Lake, we used mesocosm experiments (Paul and Schindler 1994) and a whole-lake manipulation (McNaught and others 1999) to show that *H. arcticus* is a keystone species in fishless alpine lakes, shaping the herbivorous zooplankton communities by preying on rotifers and copepod nauplii (Anderson 1977; Anderson 1980).

In keeping with changing public attitudes (Rahel 1997), and a 1988 change in Parks Canada's mandate to maintain ecosystems in their pristine condition, stocking ceased in the mountain national parks in the late 1980s. In 1995-96, the Banff-Bow Valley Task Force was appointed by the Minister of Heritage to make recommendations for maintaining and restoring ecosystems of Banff National Park. Based on a review of the state of fisheries in Banff National Park (Schindler and Pacas 1996), the Task Force (Banff-Bow Valley Study 1996, summarized by Schindler 2000) recommended that scientific studies be undertaken to explore the feasibility of restoring aquatic communities that had been changed by the stocking of non-native species.

The proposal to remove non-native fishes in the parks provoked tremendous controversy (Ritchie 2000) even though native populations of threatened Bull Trout (*Salvelinus confluentus*) in some of the lakes were replaced by introduced species (Donald and Stelfox 1997). Several of the affected lakes in Banff National Park are internationally famous tourist destinations. Opposition arises from anglers, who often prefer introduced over native fish species, and other groups who oppose the use of fish poisons or other controversial measures to remove the fish.

In 1996, we proposed to Parks Canada that we experimentally remove Brook Trout from Bighorn Lake, as a pilot experiment to test the feasibility of using gillnets to

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[1] *A version of this chapter has been published. Parker, Schindler, Donald and Anderson 2001. Ecosystems 4: 334-345.*

remove fish in larger lakes, and to assess the degree to which the original aquatic communities might recover following fish removal. Gillnet removal of introduced salmonids was being attempted elsewhere at the same time (Knapp and Matthews 1998).

In this paper we describe the Brook Trout population of Bighorn Lake and the long-term changes in the zooplankton and phytoplankton that resulted from the food-web manipulations caused by the introduction and later removal of non-native Brook Trout. Further, we discuss the efficacy of removal of non-native trout with gillnets and its applicability to other lakes.

METHODS

Study Site

The Bighorn Lake watershed is located in the front ranges of the Canadian Rocky Mountains in Banff National Park, Canada (115°39'W:51°28'N). Because of its remote location and difficult access, human activity in the watershed is minimal. Research activities comprised all of the human use of the basin in the last decade except for occasional guided visits by small groups of tourists.

The Bighorn Lake watershed is a glacial cirque cut into stratified sedimentary bedrock that rises >700 m above the lake surface. Talus overlies the bedrock at lower elevations. Alpine tundra comprises 2 ha of the 107 ha watershed, which otherwise is nearly barren of vegetation. A rock glacier (Holland and Coen 1983) and several permanent snowfields are present above the lake. Lake environs are particularly windy due to the west-facing exposure of the catchment and its location at the end of a 5 km long hanging valley.

Bighorn Lake (2347 m asl) is 2.1 ha in area, 9.2 m deep (mean depth 3.1 m) and oligotrophic (TP 4-12 $\mu g\ L^{-1}$). The ice-free season is mid-June-early July through early October. Ice thickness reaches 1.75 m in late winter. Mean annual water temperature varied between 2.5 and 4.6°C in the 1990s, with mid-summer surface water maximum temperatures reaching 5.8-14.8°C. Under-ice water temperatures averaged between 1 and 2°C through the entire water column. Secchi depth is shallow compared to nearby lakes, averaging 3.1 m, due to fine silt in the water-column. The lake weakly stratifies for 2-3 weeks during hot summers. Stratification does not occur during cool summers. Unlike other nearby high-elevation lakes, a benthic algal mat of *Rhizoclonium hieroglyphicum* develops between 3 and 5 m depth. Otherwise, the littoral zone, which consists mostly of fractured bedrock, boulders and talus, is devoid of vegetation. Littoral areas to 2 m or more depth dry and/or freeze annually due to a 1-2 m drawdown over late summer and winter.

Surface outflow occurs for several weeks during and just after snowmelt, but most outflow occurs through fissures in bedrock at the west end of the lake. Most catchment runoff enters the lake as unquantified subsurface flow. Estimated water renewal rate, extrapolated from nearby basins where hydrologic flux has been measured, is 25 times per year. Conductivity (Figure 2.2) and concentrations of most chemical constituents are variable, probably due to a combination of high flushing rate and annually variable precipitation and glacier melt. Long-term average values for selected water chemistry parameters are provided in Table 2.1. Overall, and in common with other nearby alpine

lakes, Bighorn Lake has seasonally variable water chemistry, low nutrients, relatively hard water and moderately high alkalinity.

The Original Zooplankton Community

On first sampling in 1966, the second year of trout stocking, the calanoid copepod *H. arcticus* was the only species of crustacean zooplankton captured from Bighorn Lake (Anderson and Donald 1978). Fish predation already had impoverished the zooplankton fauna by this time. The original zooplankton community in Bighorn Lake probably was similar to that of Anderson's (1974) high-elevation Type II lakes, that were dominated by *H. arcticus*, but also contained two to three less abundant species of copepods and the cladoceran *Daphnia middendorffiana*. *Acanthocyclops vernalis*, *Diacyclops bicuspidatus* and *Leptodiaptomus tyrelli* all appeared in the plankton after *H. arcticus* was eliminated. It is probable that these species were originally present but held at low abundance due to predation by *H. arcticus*. *Daphnia* ephippia occurred in lake sediments, indicating this genus was also present prior to the introduction of fish. No rotifers were recorded in 1966 but *Keratella*, *Notholca*, *Polyarthra* and *Synchaeta* appeared by 1968-69. Again, these probably were present prior to fish stocking, but held at low densities by *Hesperodiaptomus* predation, as observed in nearby Snowflake and other lakes (Anderson 1980; Paul and Schindler 1994; McNaught and others 1999). *Gammarus lacustris*, present in all other nearby permanent waterbodies that do not freeze to the bottom, has never been recovered from Bighorn Lake. If originally present in the lake, its abundance probably was low, reflecting the lack of organic shoreline habitat.

Stocking History

Bighorn Lake was fishless prior to the introduction of 2000 fingerling Brook Trout in both 1965 and 1966. Although national park stocking records do not report the introduction of non-native Rainbow Trout (*Oncorhynchus mykiss*), several individuals were captured in 1968. Brook Trout were the only fish species present in 1977 (Anderson and Donald 1978) and later years. No Brook Trout recruitment occurred prior to 1977; all fish captured in test-netting that year were original stocked fish of age 13 or 14 (Anderson and Donald 1978). In 1977 it was believed, due to the lack of reproductive success, that the lake would return to a fishless state without further intervention. However, both juvenile and adult Brook Trout were observed in the early 1990s, indicating reproduction had commenced sometime after 1977.

Fish Removal and Life History

Brook Trout were removed with twenty-two 35 m gangs of mixed-mesh monofilament nylon gillnets (25 mm to 100 mm stretched mesh, approximately 350 m gillnet ha^{-1}) from 6-14 July 1997, then with 5 mixed-mesh gangs from July 14, 1997 until July 1, 1998, when an additional 6 mixed-mesh gangs were added (25 to 75 mm stretched mesh). We continued to fish with a minimum of ten, 35 m mixed-mesh gillnets through 2000. Nets were checked daily for the first five days, every other day for the next 5 days and once every two to four weeks thereafter. Deep-set gillnets were left to fish under the ice during winter. By August 2000, >10,000 net nights of fishing effort were devoted to fish removal. All Brook Trout carcasses were removed from the Bighorn Lake watershed.

The fork lengths (FL) of all captured Brook Trout were measured to the nearest mm (±1 mm). Mass in g (±1 g) was determined on a portable electronic balance for all but ~10% of captured trout, the latter being substantially decomposed. Means of length and mass are presented as mean ± one standard deviation. A fork length-wet mass regression was calculated for Brook Trout captured between 6 July 1997 and 27 September 1997 by which date gillnetting had removed > 75% of all Brook Trout.

A combination of otoliths and fin rays were used to estimate individual age. Otoliths were cut, then burned (Christensen 1964) prior to reading under a dissecting microscope. Fin rays were air-dried, coated in epoxy, cross-sectioned, dipped in light oil (to provide an evenly refractive surface) and examined with reflected light over a black background using a dissecting microscope. Aging of adult Brook Trout was not validated except for the 1977 sample, where assessed otolith age was consistent with the number of years elapsed since the time of stocking. Ages were difficult to interpret for some individuals, particularly those exceeding an estimated 14 years of age.

Plankton, Chlorophyll-a and Water Chemistry

Zooplankton were collected in 1966, 1968, 1971, 1972, 1977, 1991, 1992 and 1994-1999. In all years, zooplankton were sampled with 30 cm diameter (d) 64µm mesh Wisconsin style plankton nets. Prior to 1991, nets were towed twice from 1 m above the bottom to the surface. In the 1990s five similar tows were made on each date. Zooplankton were preserved with formalin through 1977 and sugar-formalin in the 1990s (Haney and Hall 1973). Zooplankton counts were not corrected for net efficiency. Rotifers and copepod nauplii were enumerated using an inverted microscope after settling subsamples (10-25% of sample volume) overnight. Large zooplankton were enumerated under a stereo dissecting microscope. Sampling frequency was once or twice a year before 1991 and has varied between 2 and 5 times per year thereafter. Access restrictions due to wildlife activity, high flows that prevented fording of rivers and creeks and occasional severe weather conditions precluded implementing a strictly defined sampling regimen.

In the 1990s phytoplankton samples were collected using a 275 cm long 5 cm d clear plastic tube and plug (DeVries and Stein 1991). Three tube samples were combined and mixed thoroughly. Two hundred and fifty ml were subsampled for phytoplankton analysis and preserved with acid Lugol's. Phytoplankton were enumerated using an inverted microscope following settling of subsamples. Wet biomass was calculated based on geometric shapes of plankton (Rott 1981) assuming a specific gravity of one. Chlorophyll-*a* (chl-*a*) was collected by filtering > 1L of tube-sampled through a GF/F glass-fibre filter. Filters were placed in a petri dish, covered in foil and stored in a creek (<6°C) until transported to the University of Alberta Limnology Library for analysis. Storage of filters for up to 4 days did not significantly affect measured chl-*a* concentration (Appendix A). Chl-*a* was extracted with 95% ethanol following the method of Welschmeyer (1994) and its concentration determined fluorometrically.

Near-surface water samples for chemical analysis were collected by plunging two, twice rinsed, 500 ml high-density polyethylene bottles to ~10 cm depth and allowing them to fill with water. The content of one bottle was immediately filtered through a GF/F filter to remove seston. The filter was retained for analysis of seston nitrogen

(seston N). Seston N was measured using a CEC 440 Elemental Analyzer. TDN was determined by colourimetric analysis of filtered lake-water following digestion of samples. TN = TDN + seston N. TP was determined colourimetrically, using the unfiltered portion of the sample, with a spectrophotometer. Samples were transported and stored as described for chl-*a* samples. Chl-*a* and water chemistry were collected in the 1990s only.

Crustacean diapausing egg banks

To assess if diapausing eggs of *H.arcticus* and/or *D.middendorffiana* were present, and thus a source of propagules to support internal recolonization of one or both species, we collected and examined Bighorn Lake sediments. Two sediment cores were collected using a 5.1 cm d trigger-released gravity corer following the methodology of Parker and others (1996). Cores were held in the dark at 2°C for two weeks prior to analysis. Cores were extruded and sectioned at 5 mm intervals to a depth of 50 mm. The outer 3 mm of each slice was removed to avoid contamination of samples due to smearing. Core slices were diluted with GF/F filtered lake water, sonicated for two minutes, then washed through a 75 µm nylon sieve, which was selected to retain diapausing eggs based on Parker and others (1996). Retained sediments were screened for *H. arcticus* resting eggs using a counting ring under a dissecting microscope. Counting efficiency was > 95% (Parker and others 1996).

In addition, 5.8 L of near surface sediments (to ~6 cm depth and covering 0.1 m^2 surface area) were collected by Ekman grab on 14 July 1997. Samples were sieved and screened for *Hesperodiaptomus* resting eggs as described above. *Daphnia* ephippia were not enumerated in sediment samples, but their occurrence was noted.

RESULTS

Fish Population

In the first week of gillnetting, 146 Brook Trout were caught. By October 1997, 192 Brook Trout were removed. The remains of 13 mature and 6 juvenile Brook Trout were removed from gillnets in June 1998. Only a single juvenile was captured during the remainder of the summer. In 1999, 48 juvenile Brook Trout of the 1996 cohort were captured by mid-July. One additional juvenile of the 1996 cohort was removed from gillnets in July 2000, by which date total catch was 261 Brook Trout. Approximately 5700 seconds of electroshocking (pulse time) with a 3.5 amp AC boat-mounted shocker on 18 July 2000 failed to yield any further Brook Trout. No additional Brook Trout were caught by any method thereafter, through 2004.

Sexually mature Brook Trout averaged 273 ± 22 mm FL (Figure 2.3) and 217 ± 46 g wet mass. Estimated standing stock on 6 July 1997 was 20.7 kg ha^{-1}. The wet mass fork length regression for all Brook Trout captured in 1997 is provided in Figure 2.4. Individual Brook Trout attained 90% or more of observed asymptotic length by age 5 (Figure 2.5). Little annual growth occurred thereafter through a life span of at least 18 years. Maximum observed FL was 340 mm. Males grew faster and exhibited greater mean size, but shorter longevity and maximum length than females. Minimum size and age at maturity in 1997 were 200 mm FL and age 5, for both sexes, but few Brook Trout under 230 mm FL had mature gonads.

Changes in the Zooplankton Community Following Trout Stocking

D.middendorffiana most likely was eliminated from the water column shortly after stocking of Brook Trout first occurred in 1965. *H.arcticus* was eliminated between 1968 and 1971 (Figure 2.6). *Diacyclops bicuspidatus* first appeared in 1968. *Acanthocyclops vernalis* were first captured in 1972 and were abundant by 1977 (Anderson and Donald 1978). By the early 1990s *Diacyclops* had replaced *Acanthocyclops* as the dominant predatory crustacean. While cyclopoid copepod nauplii were abundant after Brook Trout were introduced, densities of adults typically were $< 1\ m^{-3}$. Rotifers, primarily *Synchaeta* and *Polyarthra*, which were rare in 1966 and 1968, were abundant in the 1970s (Figure 2.7). A diverse assemblage of rotifers, including *Brachionus*, *Euchlanis*, *Filinia*, *Kellicottia*, *Keratella*, *Lecane*, *Lepadella*, *Monostylis*, *Mytilina*, *Notholca*, *Polyarthra*, *Synchaeta* and *Trichotria* occupied Bighorn Lake in the early 1990s but only *Keratella* and *Polyarthra* occurred at densities exceeding $10\ L^{-1}$.

Changes in the Zooplankton Community During Fish Removal

Despite cold water-temperatures and oligotrophic conditions, zooplankton responded to fish removal within a few weeks. Whereas when fish were present zooplankton consisted mainly of nauplius larvae of *Diacyclops* and the rotifers *Polyarthra* and *Keratella*, within 8 weeks numerous copepodids and adults of *Diacyclops* were present (Figure 2.8), causing most of the initial increase in the average size of the zooplankton (Figure 2.9). Densities of adult *Diacyclops* increased by more than 3 orders of magnitude by 1998 (Figure 2.8). The abundance of *Diacyclops* nauplii declined as adult density increased. *Diacyclops* egg counts averaged 35.4 per female in 1996 and 1997 combined. In 1998-99 average egg count was 10.2 eggs per female. There was little change in the abundance of *Acanthocyclops* following fish removal.

Daphnia middendorffiana was first collected in August 1998, more than a year after fish removal commenced. Initial observed density was $0.62\ L^{-1}$ (Figure 2.6). *Daphnia* density decreased in 1999.

In the 1990s, *Polyarthra* and *Keratella* were the most abundant genera of rotifers, together comprising > 95% of rotifer biomass. Total rotifer density was annually variable (Figure 2.7) and highest in the comparatively warm summers of 1994 and 1997.

No *H. arcticus* were captured following the commencement of fish removal. No viable *H. arcticus* resting eggs were found in the pair of sediment cores or the bulk sediment samples we examined.

Overall, the total biomass of zooplankton changed little after fish removal and remained within the range observed when fish were present (Figure 2.9).

Changes in the Phytoplankton Community during Fish Removal

Total phytoplankton biomass and chl-*a* in 1997-99 remained within or exceeded the range observed in the five years prior to Brook Trout removal (Figure 2.10). Although plankton biomass was low in 1999 compared to earlier years, this observation was consistent with the observed correlation between annual maximum phytoplankton biomass and maximum summer surface water temperature ($r^2 = 0.72$; $p < 0.03$).

Diatoms (mostly *Fragilaria* sp.) and Dinophyceae (primarily *Gymnodinium* sp.), dominated the plankton community of Bighorn Lake throughout the 1990s, comprising > 5% of the biomass of the algal flora (Figure 2.11). The most significant food web effect of fish removal on phytoplankton was the loss of chrysophytes (*Dinobryon* and *Mallomonas* sp.) and cryptophytes (*Rhodomonas* and *Katablepharis* sp) all of which were lost or decreased below detectable levels following commencement of fish removal.

Phytoplankton species < 25 µm in length declined from 40-60% to < 10% of the phytoplankton (Figure 2.12) following fish removal. Small cells were also rare in the early 1990s when no *Daphnia* were present.

Nutrient Concentrations

Average annual TP concentrations in Bighorn Lake increased from 3 to 9 µg L^{-1} between 1992 and 1998, then declined slightly in 1999 (Figure 2.13). TN measurements began in 1994. TN concentrations generally followed directional trends in TP. TN increased from 130 to 185 µg L^{-1}. There was no visible effect of fish removal on either nutrient.

DISCUSSION

Fish Population

The history of the introduced Brook Trout population in Bighorn Lake was remarkably similar to that of the same species introduced into cold, oligotrophic Bunny Lake, in the Sierra Nevadas of California (Reimers 1979). Low growth rates, among the lowest reported for numerous populations in Banff National Park (Mayhood and Anderson 1976) and elsewhere (Carlander 1969), great age and long delays prior to successful spawning, at least 12 and 16 years in Bighorn and Bunny lakes respectively, were common to both populations. Further, in both lakes second-generation trout grew larger than the original stocked cohorts (Figure 2.3), probably reflecting reduced Brook Trout abundance and thus greater per capita food availability over time. High elevation and cold water-temperatures probably were of lesser importance in explaining the low growth and mass at age of Brook Trout in Bighorn Lake than the low abundance of large prey species (Donald and others 1980).

Zooplankton Populations

Changes in the plankton community of Bighorn Lake following fish stocking and removal were similar to those observed in Snowflake (McNaught and others 1999) and Pipit (Anderson and Donald 1978; Schindler and Parker 2002) lakes and high-elevation lakes in the Sierra Nevadas (Knapp and others 2001) which were also stocked with non-native salmonids. The loss of *H. arcticus* was expected because it does not coexist with fish in small alpine and subalpine lakes (Donald and others 1994). Stocked fish probably also eliminated *Daphnia*. Cladocera also were lost from both Snowflake and Pipit Lakes following stocking with salmonids. Similar loss of *Daphnia* and/or large *Diaptomus* following fish introduction into high elevations lakes is a common response to salmonid stocking (Gliwicz 1967; Reimers 1979; Pechlaner 1984; Knapp and others 2001). Increased abundances of cyclopoid copepods following the loss of *H. arcticus* were

expected, they typically are present at high abundance when *H. arcticus* is eliminated (Anderson 1974, 1977, 1980; McNaught and others 1999).

We speculate that the return of *Daphnia* following the onset of fish removal was a result of hatching of ephippia, which we identified in lake sediments. The year-long delay in reappearance is consistent with the long recovery times for *Daphnia* observed in several Sierra Nevada lakes (Sarnelle and Knapp 2004) and the delayed proliferation of large *Daphnia* species following food web manipulations in experimentally eutrophied lakes (Elser and others 2000). The early seasonal hatching of ephippia, which in 1997 likely occurred before fish removal began, and the presence of a few residual Brook Trout in 1997 and 1998 may have been in part responsible for the delay in recovery of this species. Alternately, small egg bank size or low hatching rate of ephippia may have resulted in a long lag time before *Daphnia* abundance increased to detectable levels (Sarnelle and Knapp 2004). Our low sampling frequency (n = 5 in 1997 and n = 3 in 1998) may also have limited our ability to detect this species when its abundance was low (Arnott and others 1998).

The large increase in copepodid and adult *Diacyclops* abundance following commencement of fish removal was not expected. Although few *Diacyclops* survived to reach adult stages prior to fish removal, the absence of this species in fish stomach contents samples from Bighorn Lake and elsewhere in the region (Wilhelm and others 1999), and the proliferation of *Diacyclops* in other nearby lakes with stocked or native fish populations (McNaught and others 1999; Wilhelm and others 1999), had led to speculation that *Diacyclops* was not an important diet item for trout. Clearly however, heavy predation of *Diacyclops* commenced once individuals reached the first copepodid stage. Stomach contents samples do not necessarily reflect the importance of copepods in the diet of fish. In nearby Bow Lake, stable carbon isotopes indicated that zooplankton were important in the diet of Lake Trout, although zooplankters were rarely found in stomach contents samples (Campbell and others 2000). The decline in nauplii abundance following fish removal probably reflected a combination of increased cannibalism of nauplii by adults (McQueen 1969) and declining per capita fecundity as *Diacyclops* abundance increased.

The absence of *Gammarus* from Bighorn Lake is perplexing: the species is present in all other nearby permanent waterbodies that do not freeze to the bottom in winter. Gammarids were reduced below the level of detection by introduced trout in nearby Snowflake and Pipit Lakes (Anderson and Donald 1978, McNaught and others 1999) and were eliminated by stocked salmonids in European lakes (Pechlaner 1984, Amann 1990). It is possible that *Gammarus* was eliminated by Brook Trout in Bighorn Lake but this cannot be conclusively demonstrated because *Gammarus* does not leave subfossil remains in lake sediments. Alternately, the lack of surface water access to Bighorn Lake may have prevented colonization by *Gammarus* following the termination of the last Wisconsinan glacial advance.

H. arcticus did not return to Bighorn Lake following onset of fish removal, in common with its failure to return to stocked Snowflake Lake (McNaught and others 1999) and the failure of the congeneric *H. shoshone* to return to several formerly fish-stocked Sierra Nevada lakes (Sarnelle and Knapp 2004). Because there can be few, if any, viable *H. arcticus* resting eggs remaining in Bighorn Lake sediments, Allee effects,

via mate limitation, effectively eliminate the possibility of internal recolonization of this species from resting eggs (Sarnelle and Knapp 2004). *H. arcticus* has been functionally, if not absolutely, extirpated from Bighorn Lake.

Several factors seem likely to reduce the probability of the successful natural reinvasion of *H. arcticus* from other nearby watersheds. First, *Hesperodiaptomus* and other calanoid copepods are known to be poor dispersers (Stemberger 1995), exhibiting few transfers between even closely spaced ponds (Boileau and Hebert 1991) over relatively flat terrain. Dispersal limitation of zooplankton in alpine environments is thought to be common (Sarnell and Knapp 2004; Holzapfel 2005), perhaps due to poor connectedness of alpine watersheds and the high-elevation barriers between watersheds. Second, even if *Hesperodiaptomus* successfully dispersed to Bighorn Lake, *Diacyclops* had become well established in its absence. *Diacyclops* preys on calanoid copepod nauplii (Anderson 1970) and at high densities it potentially could prevent successful reinvasion if the number of *Hesperodiaptomus* propagules is low. Mate limitation (Sarnelle and Knapp 2004) also seems likely if natural reintroductions consist of small numbers of individuals.

Natural recovery of *Hesperodiaptomus* did not occur in nearby Snowflake Lake, that similar to Bighorn Lake was stocked with long-lived *Salvelinus* (as well as *O. mykiss* and *O. clarkii*), had abundant *Diacyclops*, and few or no live *H.arcticus* diapausing eggs in lake sediments (Parker and others 1996; McNaught and others 1999). In Pipit Lake, where natural recovery of *H. arcticus* was observed (Parker and others 1996) following the loss of a short-lived stocked *Oncorhynchus* population, there remained a large pool of viable resting eggs in lake sediments after trout were lost and propagule pressure probably was high. In addition, *Diacyclops* did not proliferate in Pipit Lake in the absence of *Hesperodiaptomus*.

H. arcticus was successfully reintroduced into Snowflake Lake following stocking of 660,000 animals (McNaught and others 1999). However, experimental reintroduction of 264,000 *H. arcticus* into Bighorn Lake in 2001 (Parker unpublished data), or at 4-fold higher density than for Snowflake Lake, failed to re-establish this species in Bighorn Lake. Reasons for the failure of the Bighorn Lake introduction remain unclear.

Trophic Cascading Interactions

Although the increase in the average size of zooplankton was as expected from trophic cascading theory (Carpenter and others 1985), there was no detectable biomass or chl-*a* response by the phytoplankton of Bighorn Lake that could be attributed to fish removal in the first three years of post-manipulation monitoring. The presence/absence of fish has long been known to influence the size structure and abundance of zooplankton populations (Hrbacek 1962, Brooks and Dodson 1965), but our results run contrary to other studies that correlated reduced planktivorous fish abundance with decreases in chl-*a* and algal biomass (Carpenter and others 1997, Vanni and others 1990, Helminen and Sarvala 1997).

Some fine-scale adjustments in phytoplankton taxa occurred, most notably the loss of chrysophytes and cryptophytes. These taxa were lost in the same year, but prior to the reappearance of *Daphnia*, suggesting that grazing by cladocerans was not entirely responsible for their decline. A decline in the relative abundance of small phytoplankton may also be due to the recovery of *Daphnia*. However, similarly low proportions of small

phytoplankton cells were observed several years prior to fish removal, when *Daphnia* were absent, thus changes in proportions of large to small phytoplankton cannot be unambiguously attributed to food web effects following trout removal.

There are several possible reasons for the weak trophic cascade response in Bighorn Lake. First, Bighorn Lake is oligotrophic. Enriched lakes are thought to exhibit stronger trophic cascades than those with low nutrient concentrations (Pace and others 1999). Second, the molar C:P ratios of seston generally were above 350:1 and higher than the range where a strong biomass response by *Daphnia* was expected (Elser and others 1998). Although large *Daphnia* reappeared, their density remained low compared to warmer, more nutrient rich systems (Elser and others 2000, Schindler and Comita 1972) and they may not have achieved sufficient density to reduce phytoplankton biomass. Third, coincident with the return of *Daphnia*, the abundance of herbivorous *Diacyclops* nauplii decreased. Compensation within herbivorous zooplankters thus may have partly mitigated the return of *Daphnia*. Fourth, the dominant zooplankter in Bighorn Lake, *Diacyclops*, is an ontogenetic omnivore; nauplii are herbivorous but the diet shifts to include small zooplankton as the animals grow. Omnivores may preclude the potential for strong cascades by feeding at multiple trophic levels (Pace and others 1999). Last, cold water-temperatures and short growing seasons may have imposed physiological constraints on the zooplankton in Bighorn Lake and prevented a strong response from occurring. Weak cascading reponses are common in manipulated oligotrophic ecosystems (Brett and Goldman 1996), thus our results are consistent with other works.

However, because our post-removal results only span three years, they must be considered preliminary. Nearby Snowflake Lake required about seven years for plankton populations to adjust following initial fish stocking (Anderson 1972) and remain in a state of flux 10 years after *H.arcticus* was introduced (McNaught and others 1999). Upper trophic levels similarly required 6-8 years to recover following removal of a stress (Schindler 1998) in eutrophication and acidification experiments at the Experimental Lakes Area (ELA). Bighorn Lake is colder than Snowflake Lake and ELA lakes and its planktonic community may respond even more slowly. For example, > 10 years were required for *Diacyclops* to become established as the dominant zooplankter in Bighorn Lake following fish introduction. Several more years of monitoring are required before definitive conclusions about the presence/absence or strength of any trophic cascade and the final state of recovery can be drawn.

Gillnetting as a Management Tool

Given the effort required to eliminate salmonids from Bighorn Lake and other small lakes (Knapp and Matthews 1998), we speculate that removal of non-native trout with gillnets alone may be impractical for large lakes. However, the 3.0 ha size limit suggested by Knapp and Matthews (1998) may be too conservative. We believe that structurally simple lakes of up to 10 ha and 10 m depth should be amenable to gillnet eradication of non-native fishes over reasonably short periods, without resorting to rotenone or other poisons, based on ongoing experimental gillnet removal of Brook Trout from alpine lakes of 10-20 ha and 10-20 m maximum depth in Banff National Park (CJ Pacas, unpublished data).

Where good access is available, the intermittent deployment of gillnets, as practiced by Knapp and Matthews (1998) and Sarnelle and Knapp (2004), should be adopted to minimize gillnet avoidance by salmonids. We have directly observed that both trout and charr began to avoid gillnets within a few hours of nets being set in several clear alpine lakes. Thus a series of net sets conducted days or weeks apart may remove fish more quickly than our continuous netting program.

If the restoration of substantially larger or deeper lakes is proposed, alternate methods of fish removal including, but not limited to, electrofishing, trapnetting on spawning grounds, disturbing spawning habitat, selective angling (Paul and others 2003), creating under-ice anoxia by addition of nutrients (see Brunskill and others 1980 for a possible method), lake drawdown and/or the application of piscicides should be given consideration in addition to, or in replacement of, gillnets. These alternate methods may be controversial, but they may be more practical when attempting to remove fish from certain lakes. Canadian national parks managers have previously used chemical agents to eradicate both native and non-native fish from at least 2 dozen mountain lakes.

The Bighorn Lake restoration work does not address several important issues associated with the removal of non-native fish and the restoration of aquatic food webs in high-elevation lakes. For example, for lakes with fish-habitable inlets and outlets (Bighorn Lake has neither), removal of non-native fish from inflowing waters and the installation of barriers to prevent their reinvasion from outflow creeks may be required. Also, selective removal of introduced fish from lakes that have one or more populations of native fish, such as Yellowstone Lake (Ruzycki and others 2003), lakes in the Flathead River watershed (Fredenberg 2002) and world-renowned Lake Louise (Mayhood and Anderson 1976), may be desirable. Use of gillnets, which are not species selective, may not be appropriate in these waters. Further, 'charismatic' non-target species such as Harlequin Ducks (*Histrionicus histrionicus*) and grizzly bears (*Ursos arctos*) might be adversely affected by restoration activities on some waterbodies. Diving birds may become entangled in gillnets and drown and bears may lose a food resource if spawning runs of non-native fish into shallow creeks are eliminated. Last, because organisms such as *Gammarus* may be extirpated, but leave no trace of their prior existence, it will be difficult to ascertain that full food-web restoration has been achieved for those lakes, probably most, that lack pre-stocking records of their original invertebrate communities. Although examination of never-stocked lakes has been used to assess the probable composition of pre-stocking invertebrate communities in stocked lakes (this Chapter; Donald and others 2001; Knapp and others 2001), such evaluation will not accurately describe the pristine communities of all lakes that might be subject to restoration.

Further experimental restoration work is required to better define the practical limits of gillnetting as a management tool and to provide alternate solutions for larger or otherwise 'difficult' stocked lakes. A better understanding of our few remaining pristine ecosystems is also needed if we wish to undo a century of past fisheries management practice and return a small suite of lakes to their natural state.

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Table 2.1: Selected Bighorn Lake water chemistry parameters. Means are concentration for all samples collected between 1991 and 1999 ± 1 standard deviation. DOC = dissolved organic carbon, TP = total phosphorous, TN = total nitrogen.

Constituent	Mean	Unit
PH	8.00 ± 0.29	
Alkalinity	1.37 ± 0.20	meq L^{-1}
Bicarbonate	81 ± 14	mg L^{-1}
Conductivity	281 ± 96	µS cm^{-2}
DOC	0.30 ± 0.19	mg L^{-1}
TP	7.1 ± 2.7	µg L^{-1}
TN	166 ± 87	µg L^{-1}
SO_4	61 ± 32	mg L^{-1}
Cl	0.28 ± 0.14	mg L^{-1}
Ca	38 ± 13	mg L^{-1}
Mg	14 ± 6.4	mg L^{-1}
K	0.32 ± 0.09	mg L^{-1}
Na	0.40 ± 0.19	mg L^{-1}
Si	0.80 ± 0.15	mg L^{-1}

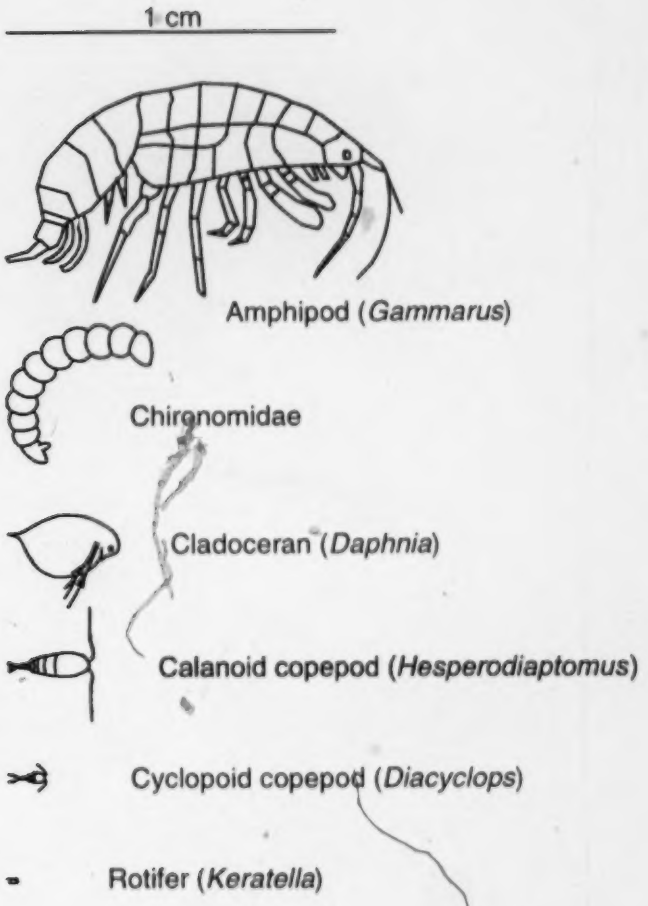

Figure 2.1: Common alpine lake invertebrates and their approximate size.

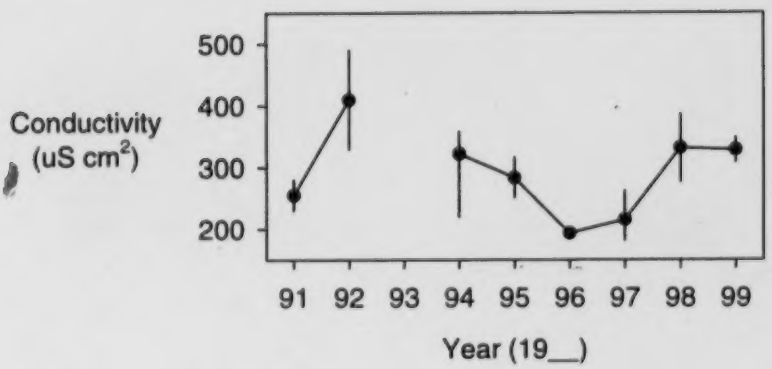

Figure 2.2: Mean conductivity with annual ranges. N = 2-5 samples year^{-1}.

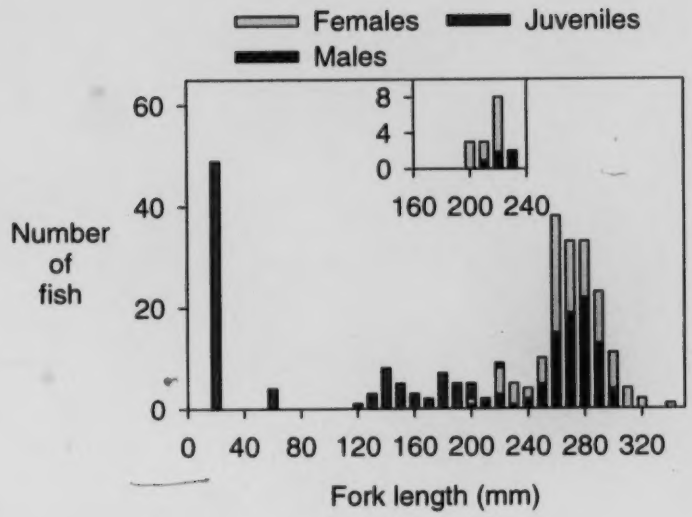

Figure 2.3: Estimated fork length distribution of Brook Trout on July 6, 1997. Trout captured in 1999 and 2000, which where young-of-year in 1997, were arbitrarily assigned a FL of 20 mm. Inset: FL distribution for Brook Trout captured in 1977.

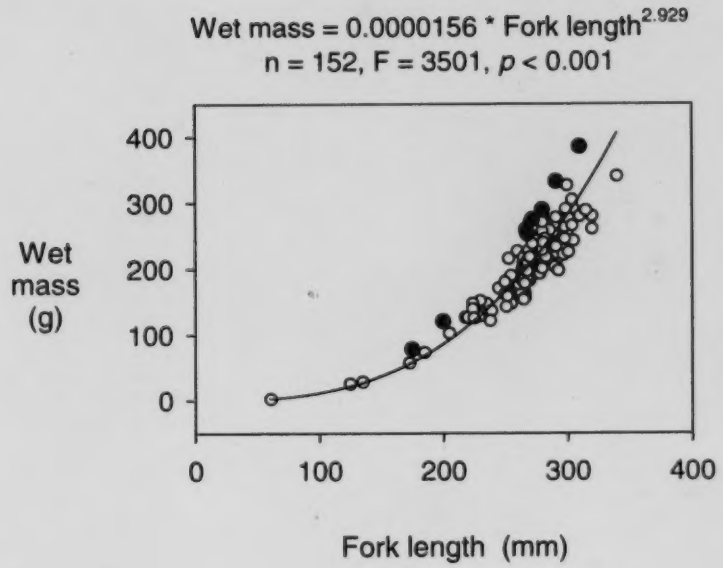

Figure 2.4: Fork length versus wet-mass for Brook Trout captured in 1997. Solid circles = Brook Trout captured in September, hollow circles = Brook Trout captured in July.

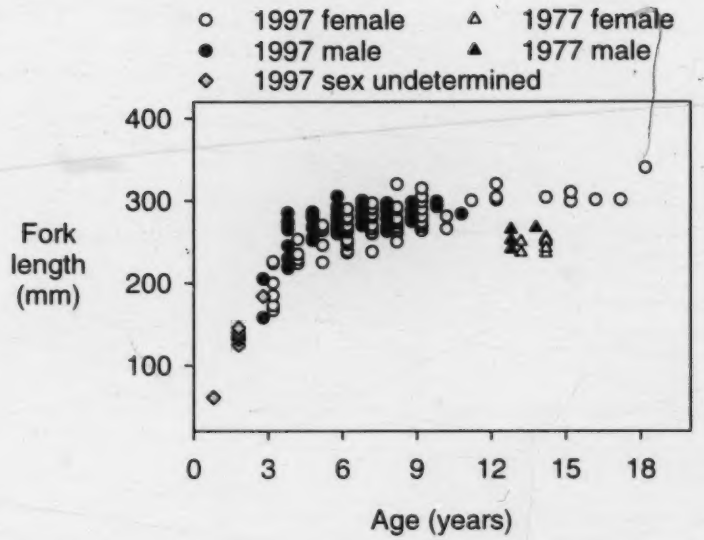

Figure 2.5: Fork length at age for Brook Trout captured in 1977 and 1997.

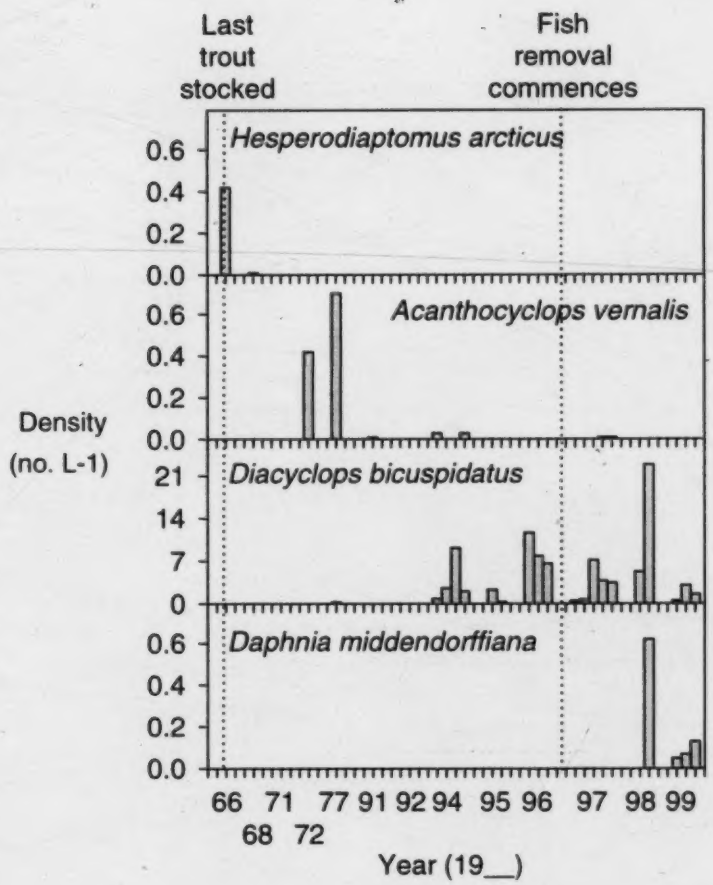

Figure 2.6: The densities of crustacean zooplankton in Bighorn Lake, 1966-1999.

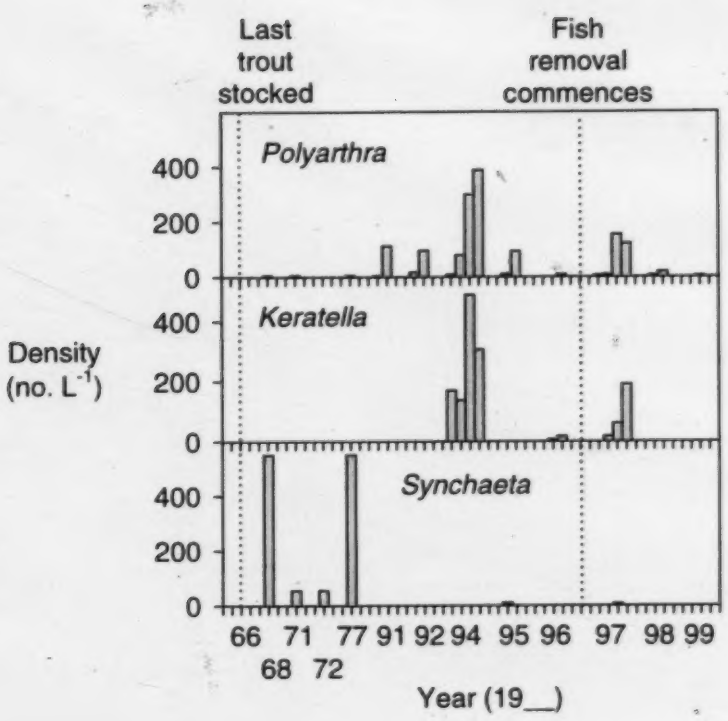

Figure 2.7: The densities of abundant rotifer genera in Bighorn Lake, 1966-1999. *Keratella* was present at low densities in the late 1960s.

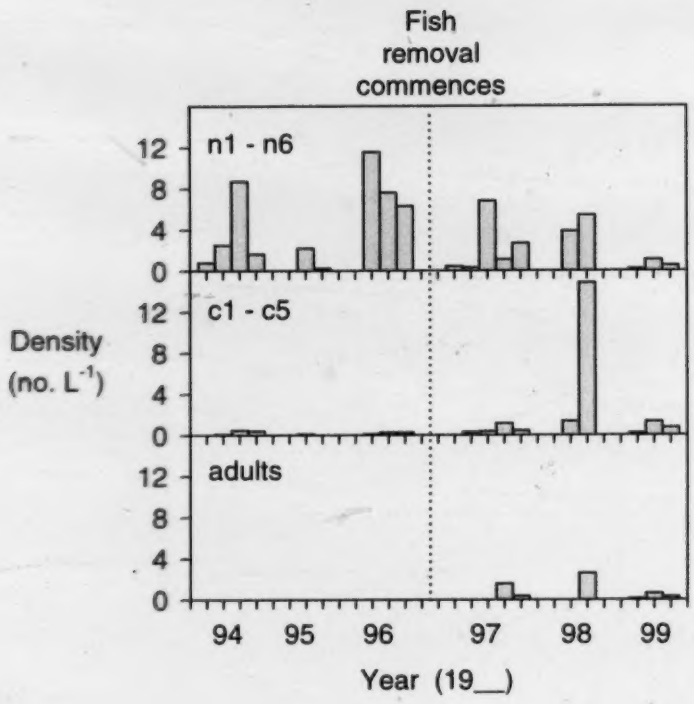

Figure 2.8: The densities of nauplius, copepodid and adult *Diacyclops bicuspidatus*, 1994-1999.

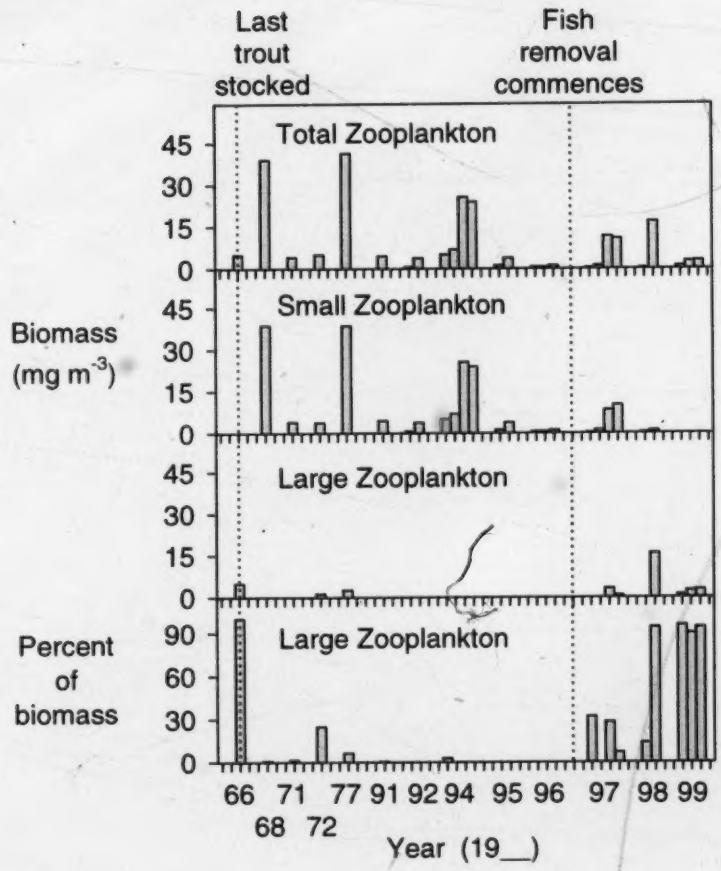

Figure 2.9: Total, small (rotifers and nauplii) and large (copepodid and adult copepods and *Daphnia*) zooplankton biomass for 1966-1999. Lower panel, large zooplankton biomass as a percent of total zooplankton biomass.

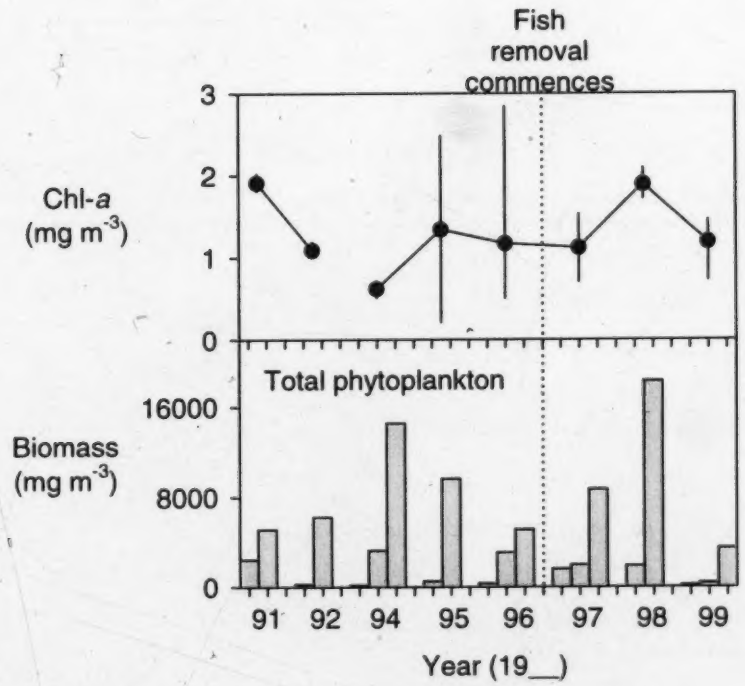

Figure 2.10: Chlorophyll-*a* concentration and total phytoplankton biomass for 1991-1999.

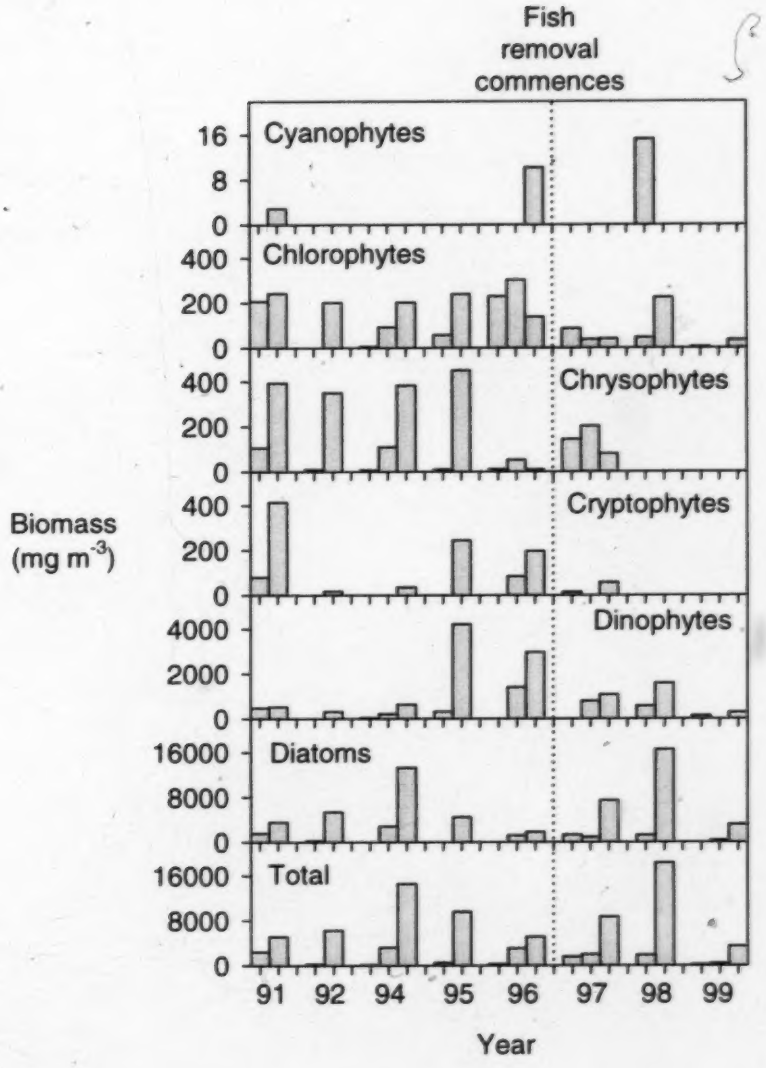

Figure 2.11: Phytoplankton biomass and chlorophyll-*a* in Bighorn Lake in the 1990s. Annual ranges are shown for chlorophyll-*a*. Ranges are less than plot symbol size in 1991 and 1992.

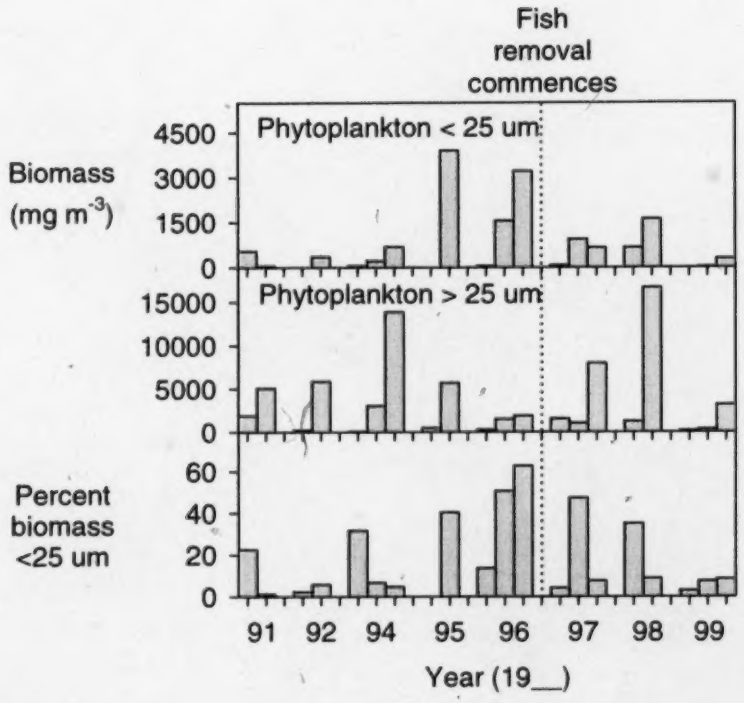

Figure 2.12: Biomass of small (<25 µm) and large (>25 µm) algal cells. Lower panel, small cell biomass as a percent of total phytoplankton biomass.

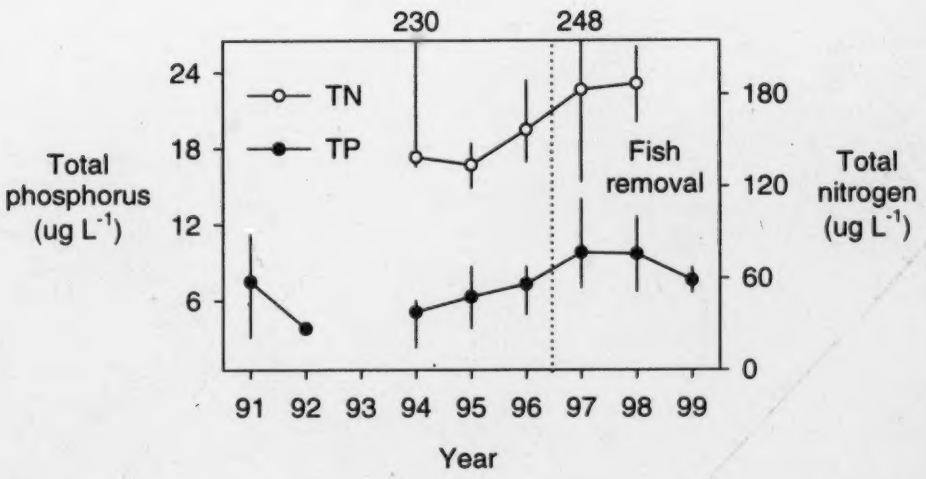

Figure 2.13: Total phosphorous and total nitrogen concentrations in lakewater. Annual mean and range provided. N = 2-5 samples year^{-1}.

CHAPTER THREE: CASCADING TROPHIC INTERACTIONS IN AN OLIGOTROPHIC, SPECIES-POOR ALPINE LAKE[2]

INTRODUCTION

Cascading trophic interaction (CTI) theory in aquatic ecosystems (Carpenter and others 1985), an extension of the earlier work of Hrbacek (1961) and Brooks and Dodson (1965), predicts that phytoplankton standing crop is regulated by the highest trophic level in a food chain. In aquatic ecosystems with an even number of trophic levels phytoplankton biomass is expected to be low, where an odd number of trophic levels is present, phytoplankton biomass should accumulate.

Although top-down cascades are reported from a diverse array of aquatic ecosystems (Carpenter and others 1987; Power 1990; Estes and others 1998), their relative strength varies widely (Brett and Goldman 1996; Pace and others 1999). In general, top-down control is thought to increase in strength as ecosystem productivity increases (Sarnelle 1992; Mazumder 1994), although some reduction in control may occur at very high productivity (Jeppeson and others 2003). Further, cascades appear to be stronger in species-poor ecosystems or those where the food web approaches a linear chain-like configuration (Power 1990; Strong 1992; Polis and others 2000). Stoichiometric constraints are also thought to limit cascading responses where seston C:P ratios are high (>350:1 by atoms) and mineral food quality for herbivorous zooplankton is low (Elser and others 1998). If CTI are strong they may cause substantial secondary effects including changes in water transparency (Jassby and others 1990), nutrient concentrations in the water column (Elser and others 2000) and gas exchange between lakes and the atmosphere (Schindler and others 1997).

Fishless high-elevation lakes in western North America tend to be unproductive, species-poor and have high seston C:P ratios. They thus possess opposing attributes with respect to predicting the strength of CTI. Many of these lakes were subject to trophic manipulation in the early to mid 20th Century when they were stocked with non-native salmonids (Bahls 1992; Schindler 2000). Although the subsequent loss of large zooplankton species from stocked lakes has been documented (Bradford and others 1998; Schindler and Parker 2002), there is little direct evidence for strong top-down regulation of phytoplankton in these lakes. Increased concentrations of algal pigments in alpine lake sediments were correlated with the presence of stocked fish in the past (Leavitt and others 1994; Schindler and others 2001), but the changes in pigment concentrations cannot be unambiguously attributed to planktonic or benthic algal responses. Experimental work fails to confirm strong CTI to the level of phytoplankton in high elevation ecosystems. Early results following experimental non-native fish removal from alpine Bighorn Lake did not support strong linkage between the zooplankton and phytoplankton (Parker and others 2001) as phytoplankton biomass remained stable even after *Daphnia* reappeared. Elser and Goldman (1991) also found the linkage between trophic levels to be weak in an oligotrophic subalpine lake. Thus, the strength of top-down regulation of the phytoplankton in these lakes remains uncertain.

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[2] A version of this chapter has been accepted for publication. Parker and Schindler. In press. Ecosystems.

To resolve this issue, we continued study of the pelagic community of alpine Bighorn Lake for 6 years following the onset of Brook Trout (*Salvelinus fontinalis*) removal. Our observations of a long, slow recovery of the planktonic community of Snowflake Lake following the reintroduction of *Hesperodiaptomus arcticus* (Schindler and Parker 2002) led us to suspect that strong food-web responses in the plankton of Bighorn Lake remained possible several years after Brook Trout removal began. We gathered and compared zooplankton, phytoplankton, water transparency and nutrient data for 5 pre-manipulation and 6 post-manipulation years from Bighorn Lake with those from nearby fishless alpine Pipit Lake, which we used as a reference ecosystem.

We hypothesized that the removal of Brook Trout would continue to result in increased zooplankton biomass and an increase in the average size of the zooplankton in Bighorn Lake, in agreement with Carpenter and others (1985) and as previously observed by Parker and others (2001). However, in consideration of the work of Sarnelle (1992), among others, and the initial lack of phytoplankton biomass and chlorophyll-*a* concentration (chl-*a*) response observed by Parker and others (2001), we hypothesized continued weak or no response in phytoplankton biomass and chl-*a* in this unproductive ecosystem. Consequently, we hypothesized that no phytoplankton-mediated changes in water transparency would occur. Further, we hypothesized that dissolved inorganic nitrogen (DIN) and total dissolved phosphorus (TDP) concentrations in lake-water would increase, as would DIN:TDP ratio, to reflect a change in zooplankton dominance from N-rich cyclopoid copepods, to P-rich cladocerans following fish removal, as noted by Brett and others (1994). Last we expected a decrease in the seston C:P ratio in Bighorn Lake as a result of the return of *Daphnia* to the seston.

METHODS

Study Sites

Bighorn Lake, a remote, 2.1 ha, 9.2 m deep, oligotrophic (TP 4-12 $\mu g\ L^{-1}$) alpine (2347 m asl) lake, is located in the front ranges of the Canadian Rocky Mountains in Banff National Park, Alberta, Canada (115°39'W:51°28'N). Ice-free seasons were 90-120 days in the 1990s/2000s. Annual maximum surface water temperature (AMSWT) varied between 5.8 and 14.8°C. Bighorn Lake weakly thermally stratified for up to 3 weeks in 1994, 1998 and 2000, but not in other years. We cannot assess if stratification occurred between 1991 and 1993. Bighorn Lake was fishless prior to the introduction of 2000 Brook Trout in both 1965 and 1966, which established a self-maintaining trout population. Research activities comprised most of the human use of the Bighorn Lake watershed in the 1990s/2000s. Recreational use is limited to visits of several hours duration by 2-3 small groups of tourists each summer.

We used remote, fishless alpine Pipit Lake (115°52'W:51°37'N, 10.6 ha, 20.6 m deep, 2217 m asl, AMSWT 6-12°C) as a reference ecosystem. Pipit Lake has a longer water residence time than Bighorn Lake (months vs. weeks) but was cut from similar bedrock and thus has similar water chemistry (Leavitt and others 1994). Weak, sometimes intermittent, thermal stratification persisted for up to 4 weeks in all years except for 1999, for which the lake did not stratify. Originally fishless, Pipit Lake was stocked with non-native Rainbow Trout (*Oncorhynchus mykiss*) and Cutthroat Trout (*O. clarkii*) from 1964-66. Neither species reproduced. The last known fish was captured in

1977 (Anderson and Donald 1978). The planktonic community recovered to its pristine state before sampling for this study commenced in 1991 (Schindler and Parker 2002). Pipit Lake has received no recreational visitors during the period of this study; research activities constituted all recent human use of the watershed.

Fish Removal

Brook Trout were removed using up to 770 m of continuously fished mixed-mesh monofilament nylon gillnets (25-100 mm stretched mesh). Gillnetting began on July 6 1997 and was terminated August 30 2001, almost 14 months after the last Brook Trout was captured in July 2000. In total, 261 Brook Trout (estimated standing biomass 43.5 kg in July 1997) were removed: 192 in 1997, 20 in 1998, 48 in July 1999 (all of the 1996 cohort) and 1 in 2000 (of the 1996 cohort). The mean fork length of adult trout was 273 mm. Full details are provided in Chapter Two. Captured fish were removed from the Bighorn Lake watershed.

To confirm eradication of Brook Trout we set two 35 m mixed-mesh gillnets (25-75 mm stretched mesh) in Bighorn Lake for the period July 12 - August 26, 2003. No Brook Trout were captured or observed and the population is considered extirpated.

Sample Collection and Analysis

We conducted a minimum of two sampling trips to each lake during the open-water seasons of the years 1991-2002 (excluding 1993 for Bighorn Lake) using a combination of foot and helicopter access. Helicopter-based sampling was more frequent for Bighorn Lake than Pipit Lake prior to 1999, due to the challenges of routinely accessing Bighorn Lake by foot. All sampling was helicopter-based after 1998.

Sampling was similar for both lakes. Zooplankton were collected with five tows of a 30 cm diameter 64 µm mesh Wisconsin-style plankton net, each tow beginning 1 m above the lake bottom and continuing to the lake surface. Zooplankton were immediately preserved with sugar-formalin solution. Rotifers and nauplii, considered small zooplankton, were enumerated using an inverted microscope after settling subsamples. Large zooplankton (copepodids and adult crustaceans) were enumerated using a stereo dissecting microscope. Zooplankton counts were not corrected for net efficiency.

Phytoplankton and chl-*a* were collected using a 275 cm long, 5 cm diameter clear plastic tube. 250 ml of the sample were removed for phytoplankton counting and immediately preserved with acid Lugol's. Phytoplankton were identified to species, enumerated and measured using an inverted microscope, after settling subsamples. Wet biomass (= biovolume) was calculated based on the geometric shapes of the plankton and assuming a specific gravity of one. We define small phytoplankton as those < 25 µm in largest dimension.

Chl-*a* was collected by filtering > 1 L of tube-sampled water through a GF/F filter. Filters were placed in a petri dish, sealed from water and light and held at < 6°C until transported to the University of Alberta Limnology Laboratory, within 8 hours (helicopter sampling) to 2-3 days (foot sampling). Chl-*a* was extracted in ethanol and its concentration determined fluorometrically following the method of Welschmeyer (1994). We tested for possible bias in chl-*a* analyses, as a result of differences in storage time between helicopter and foot-collected samples, with a timed storage experiment using

chl-*a* samples collected from both study lakes. We found no evidence for chl-*a* degradation on filters for up to 4 days of storage prior to pigment extraction (Appendix A).

Near-surface water samples for chemical analysis were collected by plunging two, twice rinsed, 500 ml high-density polyethylene bottles to ~10 cm depth and allowing them to fill with water. The contents of one bottle was immediately filtered through a GF/F filter to remove seston. The filter was retained for analysis of seston C. TDP and TP were determined colourimetrically with a spectrophotometer. NH_4 and $NO_2 + NO_3$ were determined colourimetrically with a Technicon Autoanalyzer II, using automated berthelot and cadmium reactions respectively. Seston carbon (seston C) was measured by thermal conductivity detector, using a CEC 440 Elemental Analyzer. Colour was defined as absorbance at 350 nm and measured using a spectrophotometer. Turbidity was measured in NTU using a nephelometer. Herein, DIN = $NH_4 + NO_3 + NO_2$ and seston phosphorus (seston P) = TP - TDP. Samples were transported and stored as described for chl-*a* samples.

Secchi disc depth (SDD) was measured with a 20 cm diameter black and white quadrant disc, to the nearest 0.1 m, from the shaded side of the boat. To assess correlations between SDD and turbidity, chl-*a*, colour, and phytoplankton biomass and thus infer the cause of changes in Secchi disc depth in Bighorn Lake, we performed linear regression analyses on $\log_{10}$ transformed data using the GLM procedure of SAS©.

BACIP Analyses

We tested for differences in total zooplankton and total phytoplankton biomass, chl-*a* and for the nutrients/nutrient ratios of seston C:P (by atoms), DIN, TDP and DIN:TDP (by atoms) between Bighorn and Pipit lakes, before and after fish removal, following the Before-After-Control-Impact-Pairs (BACIP) procedure of Stewart-Oaten and others (1986, 1992). For zooplankton, which we expected would increase in abundance and average size only after near complete removal of trout, we used 1991-1997 as pre-impact and 1998-2002 as post-impact years, based on our removal of > 90% of adult trout by the end of 1997. Because we did not expect a phytoplankton response until after *Daphnia* had reappeared we used 1991-1998 as pre-impact and 1999-2002 as post-impact years for our phytoplankton and chl-*a* comparisons on the basis that *D. middendorffiana* was present through the entire open-water season first beginning in 1999. We conducted two phytoplankton BACIP analyses, the first using all available data pairs, the second using only data pairs collected on days when both Pipit and Bighorn lakes were isothermal (results in []). The latter comparison excludes dates for which potential deepwater phytoplankton biomass maxima (Felip and Catalan 2002) would not have been sampled using our tube-sampler. We use the periods 1991-1998 and 1999-2002 for comparisons of nutrients because changes in nutrient ratios were not expected until the taxonomic dominance of the zooplankton shifted from copepods to cladocerans. We lack seston C:P data for 1991-1993, thus the pre-impact period was 1994-1998 for this analysis only.

Samples were matched by calendar date, to within ±7 days. Raw data was $\log_{10}$ transformed before differencing. We confirmed additivity of differences between pairs with the Tukey 'one degree of freedom' test and the lack of serial correlation in

differences with the Durbin-Watson test prior to testing for effect with a two-sample t-test as described by Stewart-Oaten and others (1986, 1992). We acknowledge this testing procedure constitutes an approximate test of significance (Stewart-Oaten and others 1986).

Bighorn Lake:Pipit Lake ratios provided are back-transformed means of the pre and post-impact ratios calculated for the BACIP analysis.

RESULTS AND DISCUSSION

Zooplankton

Prior to fish removal in the late 1990s, more than three decades following the introduction of non-native Brook Trout and the elimination of *H. arcticus* and *D. middendorffiana* from the water column (Parker and others 2001), the cyclopoid copepod *Diacyclops* and the rotifers *Polyarthra* and *Keratella* were the dominant zooplankters in Bighorn Lake. Zooplankton biomass in Bighorn Lake, often < 1 mg m^{-3} on individual sampling dates before manipulation, was low compared to reference Pipit Lake (mean biomass ratio 0.14:1). Further, in Bighorn Lake, the proportion of zooplankton biomass attributable to large zooplankton typically was < 6%, compared to consistently > 90% in Pipit Lake where *H. arcticus* and *D. middendorffiana* were the most abundant zooplankters. These observations were consistent with the commonly observed negative correlation between zooplankton size and abundance and the abundance of planktivorous fishes in lakes (Brooks and Dodson 1965; Post and McQueen 1987; Mittelbach and others 1995).

The zooplankton of Bighorn Lake strongly responded to fish removal (Figure 3.1). Densities of adult cyclopoid copepods, primarily *Diacyclops*, increased by > 3 orders of magnitude by late 1998. *D. middendorffiana* reappeared in August 1998 and, due to a combination of increasing abundance (to 3.5 animals L^{-1} by 2002) and large size (to 3.8 mm less the tail spine), comprised a majority of the biomass of the zooplankton beginning in 1999. The occurrence of chironomid larvae in the zooplankton also increased. Due to the increased abundance of adult cyclopoid copepods and larval chironomids and the return of *D. middendorffiana*, the mean Bighorn Lake:Pipit Lake zooplankton biomass ratio significantly increased (Table 3.1), to average 0.6:1, after 1997. Zooplankton biomass in Bighorn Lake steadily rose for 1999-2002 to peak at 64 mg m^{-3} in 2002. The increase in zooplankton biomass was similar to those reported in response to changes in fish populations in more productive lakes (Mittelbach and others 1995; Elser and others 1998). Further, the biomass of large zooplankton increased to > 90% of total zooplankton biomass in Bighorn Lake for every year after 1997, as observed in Pipit Lake and expected based on CTI theory (Carpenter and others 1985). We thus find support for our first hypothesis: that removal of fish would lead to increased zooplankton biomass and an increase in the average size of the zooplankton.

Phytoplankton

Before fish removal, phytoplankton biomass averaged 4890 mg m^{-3} in Bighorn Lake, and was much greater, 64:1 [74:1], than in reference Pipit Lake. In both lakes, diatoms were the dominant taxon (mostly *Fragilaria* in Bighorn Lake and *Cyclotella* in Pipit Lake), followed by the dinophytes (mostly *Gymnodinium*) and cryptophytes (mostly

Rhodomonas) (Figure 3.2). Chrysophytes were detected in all pre-manipulation collections from Bighorn Lake (mostly *Dinobryon*), but in only one sample from Pipit Lake (*Mallomonas*). The composition of the chlorophytes also varied between the lakes. In Pipit Lake, grazer-tolerant *Elaktothrix*, *Monoraphidium* and *Oocystis* were predominant. In contrast, Bighorn Lake contained smaller edible *Chlamydomonas*, *Crucigenia*, *Gloeocystis* and *Gonium* in addition to *Monoraphidium*.

The first phytoplankton response to our ecosystem manipulation of Bighorn Lake was the loss of chrysophytes and cryptophytes for 1998 and 1999. The loss of chrysophytes was not unexpected based on the near absence of this taxon from Pipit Lake in the 1990s. Because these taxa declined after >1000-fold increases in the density of adult cyclopoid copepods, but before *D. middendorffiana* was first detected, we infer that increased adult copepod abundance was responsible. The return of chrysophytes to Bighorn Lake in 2000, with *Mallomonas* replacing *Dinobryon*, and *Mallomonas*' routine appearance in Pipit Lake after 1999, was unexpected and may reflect phytoplankton community adaptation in both lakes to drier weather in the 2000s (Findlay and others 2001).

Further changes in the taxonomic composition of the phytoplankton occurred after the return of *Daphnia*, when all chlorophyte genera except *Monoraphidium* were lost from Bighorn Lake. No other grazer-resistant chlorophytes have since appeared in Bighorn Lake and its chlorophyte diversity remains low compared to Pipit Lake and other area *Daphnia* lakes. Also, among the diatoms, *Cyclotella* assumed dominance from *Fragilaria*, largely due to a massive decline in the abundance of *Fragilaria* after 1999.

Total phytoplankton biomass in Bighorn Lake declined to 0.9:1 [0.5:1] relative to Pipit Lake after the return of *D. middendorffiana*. The decline was statistically significant (Table 3.1, Figure 3.3 provides the BACIP trajectory) and far greater than expected based on an extrapolation of Sarnelle's (1992) model, which forecast a 0.2-fold decline in phytoplankton biomass ratio between low and high *Daphnia* states based on a mean 1999-2002 TP of 4.5 $\mu g\ L^{-1}$ for Bighorn Lake. The ~70-fold phytoplankton response exceeded the strongest responses reviewed by Brett and Goldman (1996) for CTI experiments that manipulated the abundance of planktivorous fishes. We thus reject our hypothesis that declines in phytoplankton biomass due to ecosystem manipulation would be small.

Following the return of *D. middendorffiana* to Bighorn Lake, the proportion of small phytoplankton cells increased from a pre-manipulation mean of 18% to average 77% after 1999, and approached the 12-year mean of 82% observed in Pipit Lake. Elsewhere, the average size of the phytoplankton either increased (Mittelbach and others 1995) or decreased (Carpenter and others 1987) in response to heavy grazing pressure. Although large inedible cyanophytes can increase in abundance when *Daphnia* herbivory is high (Lynch and Shapiro 1982), cyanophytes did not respond strongly to our manipulation of Bighorn Lake. Cyanophytes remained irregularly present at low biomass after our manipulation, as they did in reference Pipit Lake for the same period.

Chlorophyll-a

Although average Bighorn Lake:Pipit Lake chl-*a* ratios fell from 2.4:1 prior to 1999 to 1.6:1 following the return of *Daphnia*, the pre and post-*Daphnia* ratios were not

significantly different (Table 3.1) (Figure 3.4) and we accept our hypothesis that chl-*a* would not respond to ecosystem manipulation. Many factors potentially act to decouple chl-*a* and phytoplankton biomass responses to CTI. The chl-*a* content of algal cells is known to vary inversely with cell size (Augustf 1991), cell age (Messer and Ben Shaul 1972) and light environment (Falkowski and Owens 1980) and increase with nutrient availability (Hunter and Laws 1981). We directly measured changes in average cell size and light environment and infer reduction in mean cell age and an increase in per capita nutrient availability due to increased herbivory as a result of our trophic manipulation. We presume a combination of these factors, with all but changes in light environment favouring an increase in cellular chl-*a* content, limited the chl-*a* response in Bighorn Lake.

Although we earlier accepted, based on biomass data, that strong cascades may occur in oligotrophic lakes, our chl-*a* data are consistent with recent multi-lake surveys that showed limited response of chl-*a* to the presence/absence or composition of fish stocks in oligotrophic lakes (Drenner and Hambright 2002; Jeppesen and others 2003). In the absence of published biomass data we cannot assess whether the phytoplankton responses observed in these studies were qualitatively similar to or different from those we observed in Bighorn Lake. Because the choice of response variable may influence the interpretation of experimental work in some instances (Felip and Catalan 2000; Schmitz and others 2000), we argue for the reporting of both chl-*a* and phytoplankton biomass data in future studies of CTI, to allow better definition of the similarities and differences among ecosystems.

Water Transparency

Secchi disc depth (SDD) in Bighorn Lake averaged 3.1 m and varied little between 1991 and 1999 (Figure 3.5). Commencing in 2000, SDDs deepened in mid-late summer each year and in 2001 and 2002 the Secchi disc was clearly visible sitting on the lake bottom at 9.2 m, the lake's maximum depth. Reported SDDs were thus conservative measures of water transparency. In contrast, SDDs were comparatively stable through time for Pipit Lake.

Although SDDs increased following the manipulation of fish elsewhere (Jassby and others 1990; Brett and others 1994), associated reductions in phytoplankton biomass probably were not the cause of increased mid-summer water transparency in Bighorn Lake. Neither phytoplankton biomass nor chl-*a* was significantly correlated with SDD or turbidity (Table 3.2). However, SDD and turbidity were highly correlated (Table 3.2). As a result we infer that suspended inorganic particles, possibly rock flour, probably controlled SDD in Bighorn Lake. Thus we accept our hypothesis that no change in SDD would result from changes in the phytoplankton.

Instead, we propose that post-manipulation increases in SDD were due to increased filtering and incorporation of suspended inorganic particles into zooplankton fecal materials, which quickly settle to the sediments, as the biomass of zooplankton increased. Zooplankton were similarly implicated in the removal of suspended inorganic particles from the water column of alpine Bow Lake (Smith and Syvitski 1982). Shallow spring SDDs in all years likely were due to high inorganic sediment inputs associated with spring runoff. Transparency increased in mid-summer each year after fish removal

probably due to a combination of seasonally lower inorganic sediment inputs, comparatively high mid-summer *Daphnia* density and higher *Daphnia* filtering rates, the latter in response to warmer water temperatures (Burns 1969). In the absence of *Daphnia* in the 1990s, SDD remained shallow throughout the summer.

Alternatively, inputs of filtered subsurface water were higher in relative proportion to surface runoff in the drier summers of the 2000s, and may have contributed to increased SDD. However, mid-season SDDs reached maximum lake depth in later, wetter summers (Parker unpublished data), suggesting to us that climate effects played a smaller role in determining SDD than changes in biota as a result of the fish removal.

SDD in reference Pipit Lake was similarly unaffected by changes in the phytoplankton. As for Bighorn Lake, neither SDD nor turbidity were significantly correlated with phytoplankton biomass or chl-*a* (Table 3.2). SDD was significantly correlated only with turbidity (Table 3.2).

Nutrients

Although DIN and DIN:TDP increased after manipulation in Bighorn Lake (Figure 3.6), as shown for a small eutrophic lake (Elser and others 2000) and in mesocosm experiments in oligotrophic waters (Brett and others 1994), similar trends were observed in Pipit and other nearby lakes (Schindler and Parker unpublished data). Thus, contrary to our hypotheses, increased zooplankton biomass and change in zooplankton dominance from N-rich copepods to P-rich *Daphnia* in Bighorn Lake did not lead to increased DIN or DIN:TDP ratio (Table 3.2) in the water column relative to Pipit Lake, where zooplankton biomass varied little and dominance by copepods was continuous. Nor did TDP concentration, which fell in both lakes, increase relative to Pipit Lake (Table 3.2). Because both lakes responded similarly over time, regardless of their initial or eventual zooplankton composition or biomass, we suggest that drier climate in more recent years may have played an important role in driving DIN and TDP dynamics and overwhelmed any responses due to changes in the food web. Drier climate increases water renewal times, which are associated with reduced TDP and increased dissolved nitrogen concentrations in lakewater in boreal lakes (Schindler and others 1996).

Although seston C:P fell in Bighorn Lake relative to Pipit Lake (Figure 3.6), as we hypothesized if the abundance of *Daphnia* increased, we could not detect a statistically significant effect of manipulation (Table 3.2) due to the high variability in the ratio in both lakes. Seston C:P ratios were high and generally exceeded 350:1 for Bighorn Lake and 500:1 for Pipit Lake. Clearly, large *Daphnia* proliferated and strong CTI occurred in Bighorn Lake despite the high seston C:P ratio (Elser and others 1998). High seston C:P may have been in part responsible for the slow increase in *Daphnia* abundance in Bighorn Lake, as observed elsewhere in mesocosm experiments (Makino and others 2002), but it was not sufficient to prevent the eventual mediation of strong CTI by *Daphnia*.

CONCLUDING REMARKS

We conclude, on the basis of an increase in the zooplankton biomass ratio and a decrease in the phytoplankton biomass ratio between manipulated Bighorn Lake and reference Pipit Lake, and changes in the taxonomy and size structure of the zooplankton and phytoplankton in Bighorn Lake, that strong top-down CTI can occur in the planktonic

communities of oligotrophic, species-poor, high seston C:P lakes. Although we infer that increased cyclopoid copepod abundance following fish removal initiated several taxonomic responses in the phytoplankton, the reappearance and proliferation of large *D. middendorffiana* appears to have played the primary role in mediating the phytoplankton biomass response in Bighorn Lake. We document one indirect effect of trophic manipulation, a mid-summer increase in water transparency, probably mediated by increased zooplankton filtering of suspended inorganic particles from the water column. We found no evidence for CTI-mediated changes in dissolved nutrient concentrations in lake-water.

Notably, the phytoplankton biomass response, although eventually massive, was delayed until the third summer following the onset of fish removal and the second year following the return of *Daphnia*. Slow *Daphnia* population growth, probably as a result of a combination of delayed removal of the 1996 Brook Trout cohort, cold water temperatures, short growing seasons and perhaps high seston C:P ratios likely was responsible. Differences in interpretation of the strength of CTI between this manuscript and Parker and others (2001) are reflective of long response times and highlight the need for extended post-manipulation study in similar ecosystems.

The 70-fold phytoplankton biomass response was unexpectedly high compared to that reported for other ecosystem and mesocosm experiments. We offer several possible reasons for the strong CTI. First, the trophic manipulations of Bighorn Lake were powerful, involving the complete elimination of *D. middendorffiana* and *H. arcticus* from the water column after Brook Trout were introduced and the later extirpation of Brook Trout. The lack of a predation refuge for large zooplankton species (Donald and others 1994) and large terrestrial and benthic food subsidies to the Brook Trout (> 50% and > 40% of Brook Trout diet respectively, Anderson and Donald 1978) no doubt were important in achieving elimination of the large zooplankton after trout were introduced. Our study supports Polis' (1999) opinion that top predators that cause strong CTI generally are beneficiaries of external resource subsidization.

The strong species manipulations were compounded by a lack of species richness in fish and herbivorous crustacean zooplankton, for which only a single species of each was present. Lack of redundancy precluded compensatory species shifts that might have otherwise moderated the strong CTI and instead resulted in the loss or addition of important functional groups from the short chain-like food-web. Even among the comparatively speciose phytoplankton, grazer-susceptible taxa were lost with little compensation by grazer-tolerant species, at least in the short term of this study. Our work supports the hypotheses that low species-richness and a short chain-like food-web promote strong CTI (Power 1990; Strong 1992; Polis and others 2000).

It is possible that one or two crustacean zooplankton species and several grazer-tolerant phytoplankters will eventually invade Bighorn Lake, based on these species presence in other nearby lakes. If *H. arcticus*, the dominant zooplankter in Bighorn Lake prior to fish stocking, is among them we expect a further restructuring of the planktonic community that includes the near elimination of cyclopoid copepods, a reduction in the diversity and abundance of rotifers, a reduction in *Daphnia* abundance and further changes in the composition of the phytoplankon (McNaught and others 1999; Schindler and Parker 2002). However, it remains to be seen if *H. arcticus* or another invader can

mitigate the massive CTI we have documented to date.

Our findings support other reports (Leavitt and others 1994; Bradford and others 1998; Schindler and others 2001) that trout stocking in the early-mid 20th Century may have caused strong food web effects in stocked high-elevation lakes in western North America. Recent reductions in salmonid stocking, the resulting failure of some salmonid populations, and limited active removal of non-native fish populations (Knapp and Matthews 1998) should lead to the partial or full recovery of natural zooplankton assemblages (Donald and others 2001) in a portion of these lakes over the next few decades. Strong phytoplankton responses are possible in some cases. However, we expect these phytoplankton responses to changing fisheries management regimes, whether strong or weak, to proceed largely undocumented due to the paucity of research at high-elevation sites.

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Table 3.1: Bighorn Lake:Pipit Lake BACIP results. Total phytoplankton biomass (1) = all available data utilized. Total phytoplankton biomass (2) = data from periods when both lakes were mixing utilized. Pre-post periods defined in Methods.

Variable	*df*	*T*-statistic	*p*
Total phytoplankton biomass (1)	21	2.89	<0.01
Total Phytoplankton biomass (2)	17	2.92	<0.01
Total zooplankton biomass	21	2.36	0.03
Chl-*a*	11	0.20	0.84
TDP	18	0.89	0.38
DIN	20	0.25	0.80
DIN:TDP	13	0.61	0.55
SuspC:Susp P	8	1.33	0.22

Table 3.2: Regression analysis results for correlations between phytoplankton biomass (PB), chl-*a*, turbidity and Secchi disc depth (SDD) for Bighorn and Pipit lakes.

Independent variable	Dependent variable	*n*	Correlation coefficient	*F*-statistic	*p*
Bighorn Lake					
PB	SDD	13	0.10	2.38	0.15
Chl-*a*	SDD	11	0.04	0.59	0.47
PB	Turbidity	18	0.05	0.06	0.80
Chl-*a*	Turbidity	14	0.20	4.42	0.07
Turbidity	SDD	13	0.85	18.51	<0.01
Pipit Lake					
PB	SDD	33	0.06	3.13	0.09
Chl-*a*	SDD	32	0.03	0.01	0.89
PB	Turbidity	33	0.07	3.49	0.07
Chl-*a*	Turbidity	32	0.01	0.41	0.64
Turbidity	SDD	77	0.34	40.1	<0.01

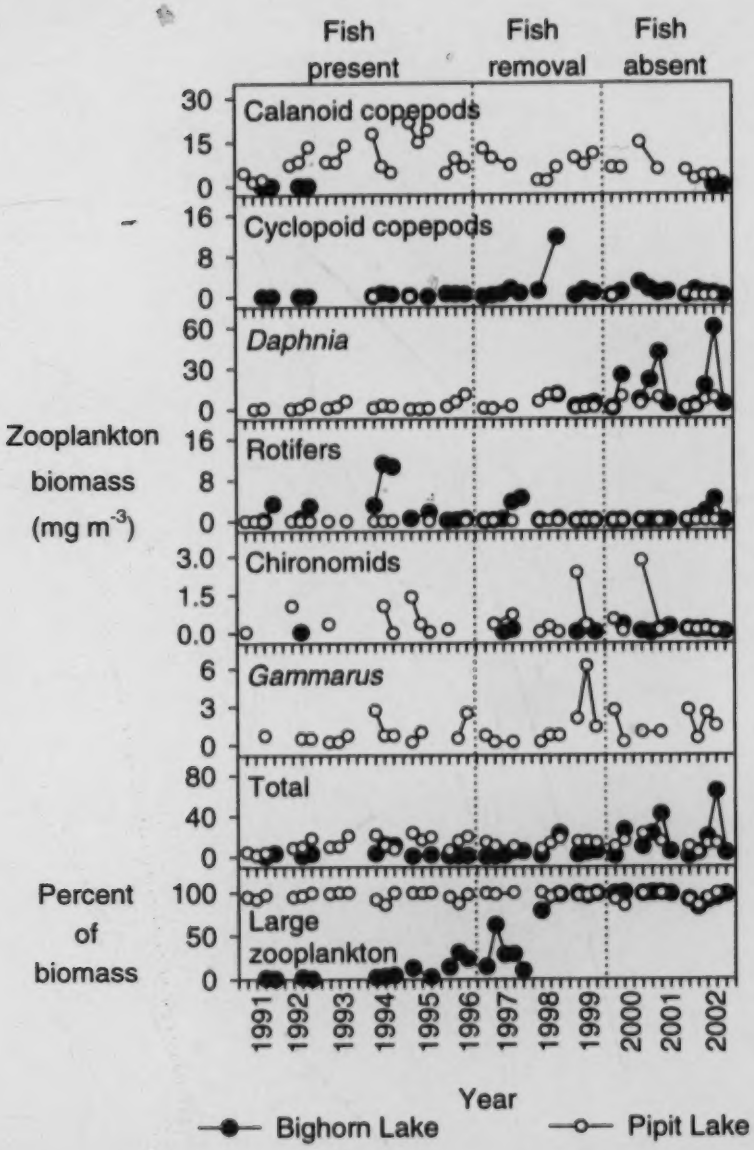

Figure 3.1: Zooplankton biomass in Bighorn and Pipit lakes. *Leptodiaptomus tyrelli* was the only calanoid copepod present in Bighorn Lake after 1990, *H. arcticus* the only calanoid in Pipit Lake. Cyclopoid copepods include *Diacyclops* and *Acanthocyclops* in Bighorn Lake, but only *Acanthocyclops* in Pipit Lake. *D. middendorffiana* is the only cladoceran known to occur in both lakes. Rotifers include *Brachionus*, *Euchlanis*, *Filinia*, *Kellicottia*, *Keratella*, *Lecane*, *Lepadella*, *Monostylis*, *Mytilina*, *Notholca*, *Polyarthra* and *Synchaeta* in Bighorn Lake and *Kellicottia*, *Keratella*, *Notholca* and *Polyarthra* in Pipit Lake. *Gammarus* is not known from Bighorn Lake. Bighorn Lake was not sampled in 1993. Missing symbol = taxon absent on date of collection.

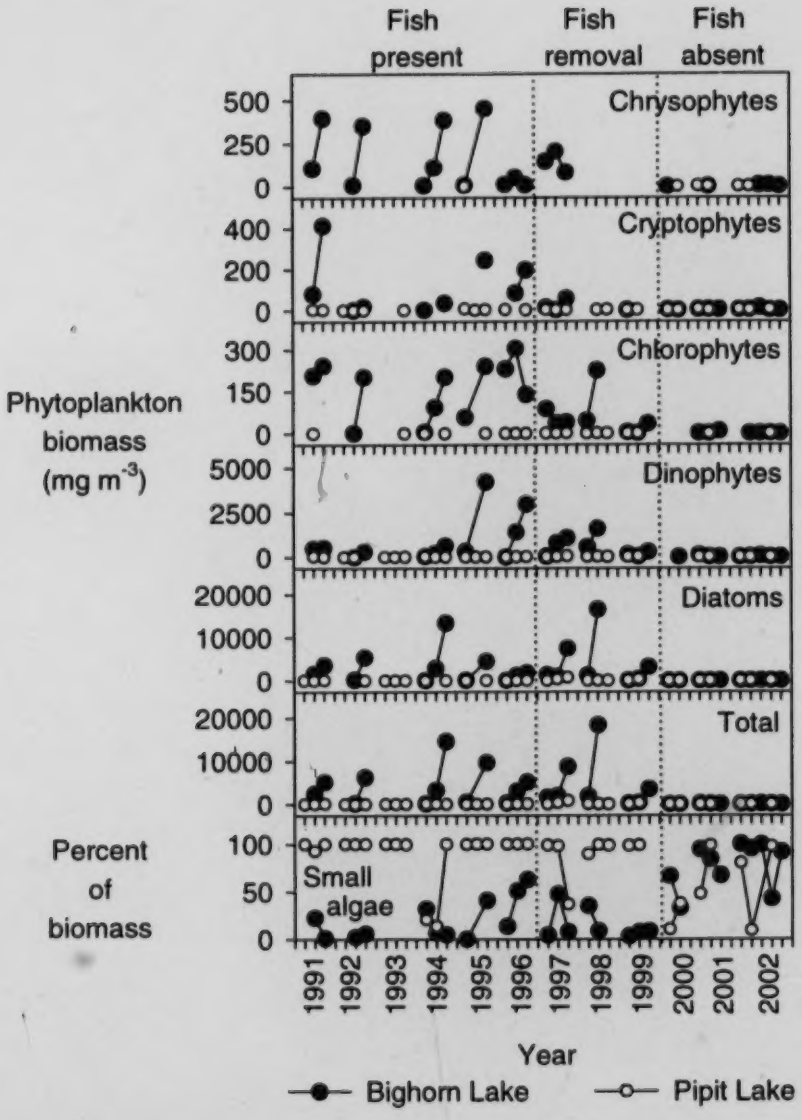

Figure 3.2: Phytoplankton biomass in Bighorn and Pipit lakes. Missing symbol = taxon absent on date of collection. Bighorn Lake was not sampled in 1993.

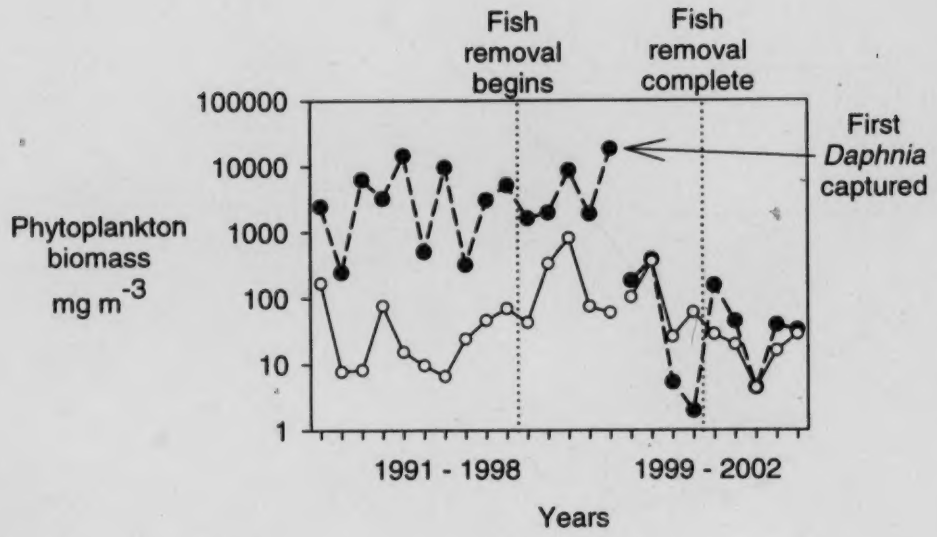

Figure 3.3: Phytoplankton biomass BACIP trajectory.

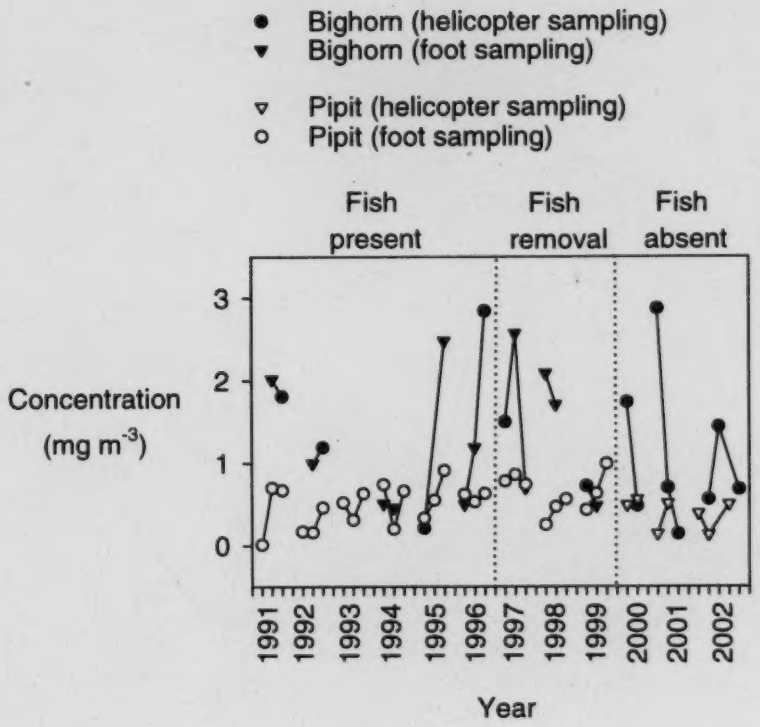

Figure 3.4: Chl-*a* concentration in Bighorn and Pipit lakes. Bighorn Lake was not sampled in 1993.

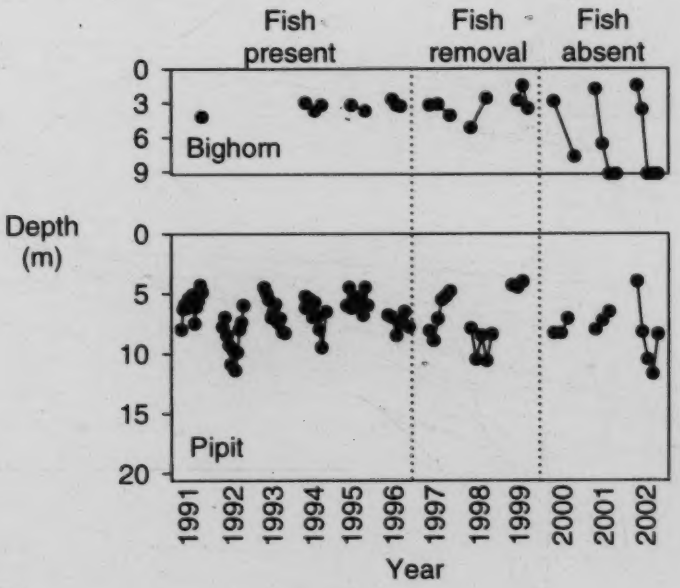

Figure 3.5: Secchi disc depth for Bighorn and Pipit lakes. The bottom of each plot is maximum lake depth.

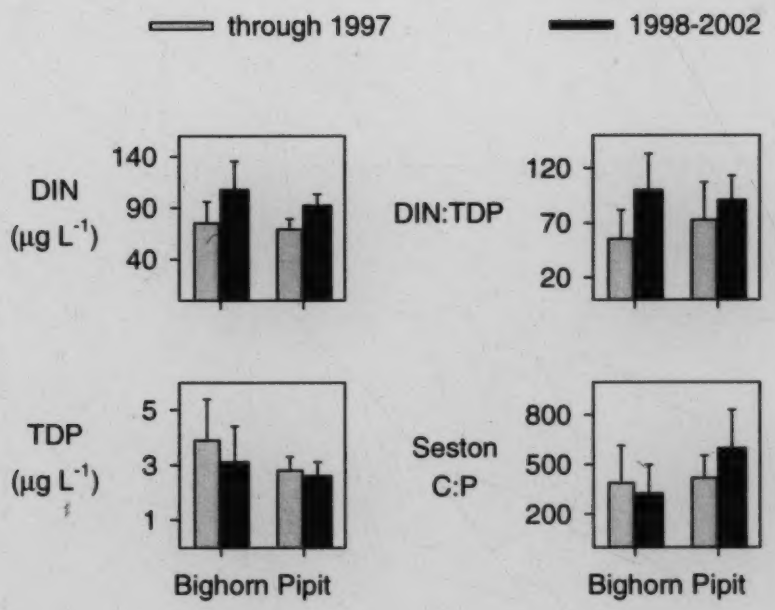

Figure 3.6: Mean DIN and TDP concentration, DIN:TDP ratio (by atoms) and seston C:P ratios (by atoms) for Bighorn and Pipit. Error bars = 95% confidence limits.

CHAPTER FOUR: BULL TROUT POPULATION RESPONSES TO REDUCTIONS IN ANGLER EFFORT AND BAG LIMITS

INTRODUCTION

The Bull Trout (*Salvelinus confluentus*) was a widespread and abundant charr of the inland waters of the northwestern United States and western Canada. Due to a combination of active Bull Trout replacement (Colpitts 1997), over-harvest (Fitch 1997), habitat disturbance (Fitch 1997) and the introduction of Brook Trout (*S. fontinalis*), Lake Trout (*S. namaycush*) and Brown trout (*Salmo trutta*) into Bull Trout waters (Donald and Stelfox 1997), the geographic range of Bull Trout has contracted (McCart 1997; Post and Johnston 2002). Numerous populations have collapsed (McCart 1997) or been eliminated (Donald and Alger 1993; Donald and Stelfox 1997; Nelson and others 2002). The Bull Trout has been variously listed as "a species of special concern", "sensitve", "vulnerable" or "endangered" through much of its range (Lohr and others 2001).

In response to the decline in Bull Trout abundance, the listing of the species and a renewed appreciation of native fish by anglers and biologists (Rahel 1997; Stuart and others 1997), new Bull Trout management and recovery plans have been instituted or are in the planning phase in many jurisdictions (Berry 1994; Lohr and others 2001; Pollard and Down 2001). Among their goals is a reduction in angling mortality of Bull Trout in waters where anglers are thought to be wholly or partly responsible for reduced Bull Trout abundance. Reducing angling mortality may be achieved by limiting angler access to water-bodies that contain Bull Trout, by imposing stringent retention limits or catch-and-release angling (CR), or both. Restricting access is thought to be an important management tool because regulating bag limits does not restrict total harvest or incidental kill (Post and others 2003). Limited angler access to Bull Trout lakes is positively associated with the long-term persistence of Bull Trout populations in Canadian mountain lakes (Donald and Stelfox 1997).

Little is known about Bull Trout population recovery following reductions in angling mortality. Although the abundance of several adfluvial Bull Trout populations in Alberta increased following prohibition of angling (Herman 1997) or the imposition of CR regulations (Mushens and others 2001), over-exploited fish stocks do not always respond quickly to reduced fishing mortality (Hutchings 2001) and several depensatory mechanisms may impede their recovery (Shelton and Healey 1999; Heikinheimo 2001; Post and others 2001). If abundance does increase following reductions in mortality, competition for resources among individuals should increase, potentially leading to one or both of decreased growth rate and fecundity (Healey 1978a, 1978b, 1980; Donald and Alger 1989).

If recruitment increases after fishing mortality declines, the potential also exists for strong interactions between cohorts originating when fishing mortality was high and those recruited when fishing mortality was reduced or eliminated. For omnivorous Bull Trout, post-fishing recruits may comprise a food resource for older and larger individuals, be competitors for the same food resources, or both. Strong inter-cohort interactions among fish can lead to rapid, often cyclic, changes in population age and size structure (Hamrin and Perrson 1986; Claessen and others 2000; Post and others 2000).

In this chapter we consider evidence for abundance change in two small Bull Trout populations in the Canadian Rocky Mountains following the progressive implementation of bag limit and access restrictions beginning in the late 1980s. We hypothesized that reduced angling mortality following regulatory changes would result in increased Bull Trout population sizes, as determined by a comparison of historic (1977-1980) and recent (1997-2001) gillnet catch-per-unit-effort and mark-recapture population estimation. We test for changes in Bull Trout growth rates to indirectly support estimated changes in population abundance. In the case of Harrison Lake alone, we hypothesized that the loss of at least 15 year-classes of large, old Bull Trout after the implementation of CR regulations was due to asymmetric size-based competitive interactions between large Bull Trout recruited to pelagic waters before and small Bull Trout recruited after the implementation of restrictive angling regimes.

METHODS

Study sites

Harrison Lake (115°, 48' W: 51°, 32' N) is an 8.4 ha, 10.7 m deep, oligotrophic (total phosphorus 4-9 $\mu g\ L^{-1}$), transparent (Secchi disk depth 3-10+m), alpine (2243 m asl) headwater lake located in the front ranges of the Rocky Mountains of Banff National Park (BNP), Alberta, Canada. Wilhelm and others (1999) describe the physical features and limnology of the lake in detail. Harrison Lake contains a presumed native, lake-resident (spawning and all life stages occur in the lake), population of 400-500 genetically uniform (lacking micro-satellite DNA diversity; Costello and others 2003) Bull Trout (excluding young-of-year and yearling Bull Trout). Bull Trout are believed to have gained access to Harrison Lake shortly after the termination of the last glaciation and before the exposure of downstream waterfalls via the erosion of valley-bottom till deposits. The population currently is closed: none of the lake inflows are habitable because of low and intermittent flow and an impassable waterfall 20 m below the lake outlet prevents immigration. Emigration of Bull Trout has not been evaluated. Harrison Lake has never been stocked. No other fish species were present during this study.

Osprey Lake (117°, 40' W: 52°, 33' N) is a 3.4 ha, 7.5 m deep, oligotrophic (total phosphorus 3-14 $\mu g\ L^{-1}$), opaque (Secchi disk depth <2 m due to glacial flour), spring-fed montane (1347 m asl) lake located in the main ranges of the Rocky Mountains in Jasper National Park (JNP), Alberta, Canada. Despite its low elevation, the lake's surface water temperature rarely exceeds 6°C, probably due to a combination of cold inflows (≤ 5°C) and short water renewal time (< 2 weeks). Osprey Lake contains a native adfluvial Bull Trout population (juveniles rear in inflow and outflow streams) of ~50 individuals (excluding Bull Trout of < age 3). The population is open: seasonal immigration and emigration may occur via the lake outflow. Osprey Lake was stocked with Rainbow Trout (*Oncorhynchus mykiss*) in 1937 and Splake (*S. namaycush* X *S. fontinalis*) and Arctic Grayling (*Thymallus arcticus*) in 1954 (Ward 1974). Only Bull Trout were present when sampling began in 1979. A single Brook Trout-Bull Trout hybrid was collected from Osprey Lake in 2001. Brook Trout were invading the outflow stream in 2002 (W Hughson, personal communication).

Angler effort and fishing regulations

No lake-specific statistical measures of angling effort are available for either lake, thus angling effort must be inferred from the few available proxy measures. These include, for both lakes, a combination of mountain national park fishing license sales records and the availability of road access. For Harrison Lake, two additional proxy measures of angler effort are available after 1978: the number of random camping (RCP, 1979-1992) and horse-grazing permits (1990-2001) issued to backcountry travelers. Visitors to Harrison Lake required one of these permits. We report the number of RCPs for all wilderness areas in BNP, including but not exclusive to the Harrison Lake watershed (because RCP holders were not required to identify exact campsite locations). For horse-grazing permits, we report the number of user-nights/year for the Upper Panther River and Windy Cabin horse-campsites, the most likely staging points for anglers continuing to Harrison Lake. Oral history reports of past recreational (Everts 2002) and commercially guided travel in the vicinity of Harrison Lake are also available.

Daily retention and multiple-day possession limits for Bull Trout were extracted from annually published fishing regulation guides.

Bull Trout sampling and handling

For 1977-80, Bull Trout were collected from Harrison and Osprey lakes using timed sets of mixed-mesh gillnets of 50-115 m length and constructed of equal length panels of 25, 38, 51, 76 and 102 mm stretched-mesh monofilament nylon net. Harrison Lake was sampled on 17 August 1977 (Anderson and Donald 1978) and 4 July 1979 (DB Donald personal communication). For Osprey Lake, Bull Trout were sampled on 1 June and 29 September 1979 (Donald and DeHenau 1981) and 18- 20 May and 18 June 1980 (DB Donald personal communication). A portion of the captured Bull Trout were killed (n = 20 for Osprey Lake, n = 15 and 17 for 1977 and 1979 respectively for Harrison Lake), measured to the nearest mm fork length (FL) and weighed to the nearest gram. Ages were determined for all sacrificed Bull Trout using otoliths. Otoliths were cleared in glycerine and examined using a dissecting microscope. Otolith ages were not validated. Sex and age at first maturity were determined by internal examination of sacrificed fish.

In the 1990s and 2000s Bull Trout were captured by angling, overnight trapnetting (trap diameter 80 cm, 25 mm stretched mesh knotless nylon, 3 m wings, 20 m lead), seining (20 m long, 2 m deep, 10 mm stretched mesh knotless nylon), dipnetting (30 cm width, 1 mm mesh aperture) and timed gillnetting (maximum set length 12 minutes). Gillnets included a combination of 17 m long, 38 mm stretched-mesh and 50 m mixed-mesh monofilament nets constructed as in the 1970s. Gear used varied among sampling days. Harrison Lake was fished on at least 7 days in each of 1997, 1998, 1999 and 2001. Osprey Lake was fished on 10 days in 2001 and 2 in 2002. Captured fish were held in 25 L holding cells for up to 30 minutes prior to processing. Aeration and water temperature in holding cells were maintained at ambient lake levels by continuous flushing with fresh lake-water. Following induction of level-3 anesthesia (Prince and Powell 2000) with either methane tricaine sulphonate (1997-1999) or clove oil/ethanol (2001), all Bull Trout were measured to the nearest mm fork length (FL) and mass determined to the nearest gram.

To determine age in the 1990s/2000s, 2-3 left pectoral fin rays were collected from 84 Harrison Lake Bull Trout and all captured Osprey Lake Bull Trout. Fin rays were air-dried, coated in epoxy, cross-sectioned, dipped in light oil (to provide an evenly refractive surface) and examined with reflected light over a black background using a dissecting microscope. Fin ray aging was validated to age 10 by comparison of left and right fin ray sections of 13 Harrison Lake and 6 Osprey Lake Bull Trout marked and left fin-clipped in one of 1997, 1998, 1999 or 2001 and recaptured and right fin-clipped in one of 1998, 1999, 2001 or 2002. Fin ray cross-sections were used to determine ages of Bull Trout up to age 12, slightly beyond the maximum validated age.

Aging using otoliths was validated to age 10 for Harrison Lake Bull Trout by comparison of otolith and validated fin ray ages for 14 Bull Trout (100-500 mm FL) deliberately sacrificed in 1997, as well as 6 unintentional gillnetting and 8 natural mortalities observed in 1997 and later years. Beyond fin ray age 13 otolith ages were 1-3 years greater than those estimated using fin rays.

To assess fecundity of pre and post-closure Bull Trout, ovaries were removed from all observed mature female mortalities, both natural and experimental. All eggs from both ovaries of each individual were enumerated and combined into a single count.

Bull Trout abundance

For Harrison Lake, for which no mark-recapture population estimate is available for the 1970s, gillnet catch per unit effort (CPUE, number of fish captured·100 m net^{-1} ·hr^{-1}) was used as an index of relative abundance change between the 1970s and 1990s/2000s. Gillnet CPUEs for 1970s samplings were based on 4-h sets of two 50 m nets (DB Donald personal communication). Log_{10} transformed gillnet CPUE for small-mesh and mixed-mesh nets were compared using a two-sample t-test to determine if catch rates varied between gillnets of different length and mesh combinations.

Mark-recapture abundance estimates for adult Bull Trout (>300 mm FL) in Harrison Lake were determined in 1997, 1999 and 2001 using the Petersen estimator (Krebs 1999). Captured and anaesthetized Bull Trout were marked with an alphanumeric-coded visible implant (VI) tag injected into the adipose tissue behind the eye and an adipose fin clip. All Bull Trout marked in the 3 months prior to the final autumn sampling date of each year, as well as any marked and recaptured Bull Trout from previous years, were considered as the initial marked sample for the Peterson population estimate.

Population abundance of Osprey Lake Bull Trout was determined using the Petersen estimator in 1980 and the Schnabel estimator (Krebs 1999) in 2001. Bull Trout captured from Osprey Lake in 1980 were marked with opercle punches or adipose fin clips (DB Donald personal communication). Twenty-two sacrificed Bull Trout were added to the 1980 population estimate. In 2001, Bull Trout were marked with VI tags and adipose fin clips. Further, gillnet CPUE is reported and described as for Harrison Lake.

In all cases 95% confidence limits within parentheses follow estimated population size.

Growth comparisons

Length-mass regressions, for 1977-79 combined and 1997, 1999 and 2001 separately, were calculated with the GLM procedure of SAS on log_{10}-transformed masses

and FLs. Z-scores (Kleinbaum and Kupper 1978) were used to compare length and mass of Harrison Lake Bull Trout of ages 5 through 10 captured in the 1970s versus those captured between 1997 and 2001. We similarly tested for differences in the same for Osprey Lake Bull Trout between 1979/1980 and 2001/2002.

Inter-cohort interactions in Harrison Lake

To determine if pre and post-closure Bull Trout competed for the same food resources, stomach contents were flushed from 32 pre-closure (born before October 1988) and 74 post-closure (born after October 1988) adult (arbitrarily those >300 mm FL) Bull Trout between 1997 and 1999. Stomachs were flushed using a technique similar to Meehan and Miller (1978) and Wilhelm and others (1999). The implementation date for restrictive regulations was arbitrarily defined as October 1988, the date when the access road was abandoned.

Stomach contents were preserved in 4% formalin until returned to the laboratory where they were transferred to and held in 70% ethanol. Contents were sorted while viewed under a dissecting microscope. Total stomach and prey category volumes for *Gammarus*, *Daphnia*, chironomids (larvae and pupae combined) other (including but not limited to Trichoptera, Ephemeroptera, Diptera, Coleoptera, oligochaetes, pelecypods, Hemiptera, Hymenoptera, water boatmen, backswimmers, mites), and Bull Trout were determined directly by water displacement. Percent stomach fullness for total stomach contents and individual prey categories for each stomach sample were estimated from:

$$\% \text{ fullness} = 100 \times \left(\frac{\text{prey volume cm}^3}{a \times \pi (a/4)^2} \right)$$

where a = distance between the origin of the pelvic and pectoral fins in cm. This calculation scales stomach contents volumes to fish size. The denominator was selected to equal or exceed the maximum measured stomach content volumes for adult Harrison Lake Bull Trout of 300-500 mm FL. The Mann-Whitney U-test (using the normal approximation (Zar 1999)) was used to test for differences in median percent stomach fullness between pre and post-closure adults. For graphical presentation, percent fullness values and absolute volumes of individual prey categories were averaged for pre and post-closure Bull Trout.

In addition, to determine if pre and post-closure Bull Trout consumed similar-sized *Daphnia*, or partitioned this prey resource on the basis of size, the length of the first 100 *Daphnia* encountered (or less if < 100 were present) was measured for all stomach contents samples that contained *Daphnia*. Length was measured from the top of the head to the base of the tail spine using an ocular micrometer equipped dissecting microscope. Mean *Daphnia* length was determined for all stomach contents samples. A grand mean was calculated for both pre and post-closure stomach contents samples.

Because Wilhelm and others (1999) found no differences in the length of *Gammarus* consumed by large and small size classes of Bull Trout we did not similarly determine the mean length of *Gammarus* consumed by pre and post-closure cohorts.

Prey biomass, density and/or size in Harrison Lake

To assess if assumed increases in the abundance of Bull Trout following fishing regulation changes were sufficient to reduce the biomass and average size of *Daphnia* in Harrison Lake, zooplankton were collected from the water column, over the deepest point of the lake using methodology and counting techniques similar to that in described for Bighorn Lake in Chapter 1. Only August zooplankton collections were used for this analysis, for which month *Daphnia* abundance and individual size reached their seasonal maximum. *Daphnia* length distributions were determined by measuring the first 100 individuals encountered. The 99th and 95th percentile lengths equal the lengths of the 2nd largest and 6th largest measured individuals respectively. A two-sample t-test, assuming unequal variances, was used to test for differences in percentile lengths between the periods 1991-1996 and 1997-2001.

We further determined the approximate 99th and 95th percentile lengths of *Daphnia* from archived zooplankton samples collected from Harrison Lake in August 1972 and August 1977. Because sample collections were comprised of fewer hauls, but using the same sampling gear, and thus contained fewer *Daphnia*, we measured 50 animals from each sample. 99th percentile length was estimated as the mean length of the two longest individuals. 95th percentile length was estimated by determining the mean of the 3rd and 4th longest individuals.

To determine benthic invertebrate abundance in 1999 and 2000, we collected 9 depth-stratified benthic grab samples with a 225 cm^2 Ekman dredge from Harrison Lake in August of both years. Samples were sieved using a 0.5 mm aperture mesh bucket and the number of chironomids and *Gammarus* counted. We report the mean density from all counts combined. Collection and sieving techniques were similar to that employed by Anderson and Donald (1978) in August 1977 and to which we compare our data.

Climate records

To determine if observed changes in Bull Trout abundance and growth rates in Harrison Lake might be attributable to directional changes in climate associated with long-term climate change and not changing management regimes, mean annual air temperature and precipitation were determined for the 10-year periods immediately preceding Bull Trout sampling in 1979 and 2001 respectively. Climate data was obtained from Banff townsite (1400 m asl), the nearest year-round weather recording station.

RESULTS

Angler effort and fishing regulations

In the late 1970s/early 1980s, both Harrison and Osprey lakes were road accessible and National Park angling license sales reached their historical high (Figure 4.1). Oral history records report high recreational use, both private and commercially guided, in the vicinity of Harrison Lake (Everts 2002).

In the 1990s, fishing license sales had declined to < 50% of their 1982 peak. RCP and grazing permit sales also declined compared to earlier years. Fire road access to Harrison Lake was closed in late 1988 but Osprey Lake remained road accessible.

For both Harrison and Osprey lakes, retention limits for Bull Trout were 10 Bull Trout·angler·day^{-1} between the mid-1950s and 1989 with possession limits of twice the

daily limit. Retention was reduced to 2 Bull Trout·angler·day^{-1}in 1990. CR regulations were imposed for Harrison Lake in 1994 and Osprey Lake in 1995. Osprey Lake was closed to angling in 1997.

Bull Trout abundance

For Harrison Lake in the 1970s, gillnet CPUE was 4.1-7.4 Bull Trout·hr^{-1}·100 m net^{-1} (mean = 5.75, n = 2) and significantly less than that of 30.5 (14.8 - 62.5) Bull Trout·hr^{-1}·100 m net^{-1} observed in 2001 for 17 m small-mesh nets (T-test, df = 8, t = 2.31, $p < 0.01$) and 30.5 (22.6 – 41.0) Bull Trout·hr^{-1}·100 m net^{-1} for 50 m mixed-mesh nets (T-test, df = 3, t = 5.55, $p = 0.011$). CPUEs were not significantly different between small and mixed-mesh nets in the latter period (T-test, df = 9, t = 0.002, $p = 0.99$).

Petersen mark-recapture abundance estimates for pelagic Bull Trout abundance (including both pre and post-closure bull trout) varied between 290 (180-670) and 350 (200-750) between 1997 and 2001 respectively. Pre-closure Bull Trout represented a small proportion of pelagic Bull Trout abundance for 1997 - 1999, when between 60 (45-94) and 54 (40-82) individuals were present. No pre-closure Bull Trout were present after 2001.

For Osprey Lake, the estimated abundances of 3-year old and older Bull Trout were similar for 1980 (31, 20-69, plus 20 sampling removals = 51) and 2001 (43, 33-66). Gillnet CPUEs of 0.54 (0.14 – 1.09) Bull Trout·hr^{-1}·100 m net^{-1} in 70-115 m mixed-mesh nets in 1979-1980 were not significantly different (T-test, df = 2, t = 0.98, $p = 0.42$), than those obtained using 50 m mixed-mesh gillnets in 2001/2002, for which CPUE was 1.47 (-0.66 – 17.7) Bull Trout·hr^{-1}·100 m net^{-1}. CPUEs for long mixed-mesh gillnets in both 1979/80 and 2001/2002 samplings were lower than for 17 m small-mesh nets in 2001/2002 for which CPUE was 5.61 (1.15 – 19.3) Bull Trout·hr^{-1}·100 m net^{-1}.

Growth and fecundity

For Harrison Lake, FL and mass at age were significantly greater (Z-test, z = 2.42, $p < 0.01$ and Z-test, z = 2.55, $p < 0.01$, respectively) in the 1970s than in the 1990s. For Bull Trout of age 5 through 10, FL was on average 23 mm and mass 326 g greater (1.3 – 2.4 fold) in the 1970s than in the 1990s/2000s (Figure 4.2). Comparing the mean mass of Bull Trout of 400-419 and 420-439 mm FL in the 1970s and 1990s/2000s, mass decreased from 915 to 757 g (17%) and 1039 to 819 g (21%) respectively.

In the 1990s, large pre-closure females had lower fecundity than all but the smallest post-closure female examined (Figure 4.3). Because collection of fecundity samples occurred over several years, and it was not clear if both pre and post-closure fecundity data should be included in a single analysis, we report only raw fecundity data.

For Osprey Lake Bull Trout, neither FL nor mass at age was significantly different between 1979/80 and 2001/02 samplings (Z-test, z = 0.36, $p = 0.35$ and Z-test, z = 1.40, $p = 0.081$ respectively). Maximum observed size was substantially greater in 2001 when a 696 mm FL individual was captured, than in 1979/1980.

Cohort replacement in Harrison Lake

In the 1990s, large pre-closure Bull Trout were emaciated compared to both pre-closure Bull Trout captured in the 1970s and post-closure Bull Trout in the 1990s (Figure

4.4). All marked and recaptured pre-closure Bull Trout exhibited either negative, no or small increment in length and all lost mass between their first and last capture (Figure 4.5). All, or a large majority of these individuals, of ages 12-26, died between October 1999 and August 2001 (Figure 4.4) based on the failure to capture individuals of this group in 2001 and later years.

In contrast to the pre-closure cohorts, the survival rate of adult post-closure Bull Trout between 1997 and 2001 was high. Assuming random distribution of marked fish, constant survival rate through time, and a 2001 adult abundance equal to the lower limit of 200, estimated annual survival for post-closure fish of > 300 mm FL and age 5-8 when first marked in 1997, was 0.92 $year^{-1}$ or similar to that observed in unexploited populations of lake trout (Mills and others 2002a). Under the same assumptions, estimated annual survival for Bull Trout of 200-300 mm FL at time of marking was 0.65 $year^{-1}$ between 1997 and 2001. In all cases, marked and recaptured Bull Trout from the former group exhibited comparatively large increases in both FL and mass between first and last capture (Figure 4.5).

The diet of both pre and post-closure Bull Trout was similar and included chironomid larvae and pupae, *Gammarus*, *Daphnia*, juvenile Bull Trout and small numbers/volumes of a wide variety of benthic and pelagic invertebrates. Percent stomach fullness, for all food items combined, of pre-closure Bull Trout (median 1.1%, mean 1.5%) was significantly lower (Mann-Whitney normal approximation, n_1 and n_2 =32 and 74 respectively, $z = -5.11$, $p < 0.01$) than observed in post-closure individuals (median 2.3%, mean 4.7%). However, the absolute volumes of food present in stomachs were similar for all food categories except *Daphnia* (Figure 4.6).

Daphnia contributed substantively only to the diet of post-closure Bull Trout, whose stomachs contents frequently contained 500-3000 individuals. In all cases, fewer than 100 *Daphnia* were found in the stomachs of pre-closure Bull Trout. The mean size of *Daphnia* consumed by pre-closure Bull Trout (2.55 mm) was significantly larger (T-test, df = 23, $t = 4.75$, $p < 0.01$) than that consumed by post-closure Bull Trout (2.30 mm) (Figure 4.7). Despite the larger size of *Daphnia* consumed by pre-closure Bull Trout the Bull Trout:*Daphnia* size ratio was higher for pre-closure Bull Trout (188:1) than for post-closure Bull Trout (175:1) (Figure 4.7).

From Wilhelm and others (1999), the modal size of *Gammarus* consumed by all size classes of Bull Trout was 9 mm. Thus approximate Bull Trout:*Gammarus* length ratios were 42:1 and 51:1 for post and pre-closure Bull Trout respectively.

Daphnia biomass and size and benthic invertebrate density

On average, *Daphnia* biomass declined by 70% comparing mean biomass from the years 1991-1996 to that of 1997-2001 (Figure 4.8). *Daphnia* biomass was also high in the 1970s. 99th and 95th percentile *Daphnia* lengths significantly decreased comparing 1991-1996 and 1997-2001, from 3.1 to 2.5 (T-test, df = 5, $t = 6.47$, $p < 0.01$) and from 2.5 to 2.3 mm (T-test, df = 4, $t = 4.81$, $p < 0.01$) respectively.

The mean densities of chironomids and *Gammarus* were 9770 and 148 m^{-2} in August 1977 and 5480 and 134 m^{-2} in 1999-2000.

Climate

For the periods 1970-79 and 1992-2001, mean annual air temperatures and annual precipitation at Banff were 2.56°C and 447 mm and 2.52°C and 448 mm, respectively. Both periods were cooler and drier than 20th Century means for annual temperature and precipitation, which were 2.66°C and 470 mm respectively.

DISCUSSION

Harrison Lake

Assuming gillnet CPUE was directly proportional to Bull Trout abundance, then adult Bull Trout abundance in Harrison Lake increased approximately 5-fold in pelagic waters, from ~65 individuals to ~320, between 1977 - 1979 and 1997 – 2001. We may under or overestimate actual abundance change to some degree if catchability was either hyperstable (Borgstrøm 1992; Harley and others 2001) or hyperdepleted (Shardlow 1993; Pierce and Tomko 2003) in the face of changing abundance. Coincident reductions in Bull Trout growth rate, with respect to both length and mass, support a substantial increase in Bull Trout abundance. Presumably, increased exploitive and/or interference competition among the Bull Trout, when their abundance increased in the late 1990s/2000s, was responsible for these compensatory biological changes. Similar responses have been reported for numerous salmonid populations subject to variable rates of exploitation (Miller 1947; Healey 1975; Healey 1980; Langeland 1986; Donald and Alger 1989; Ferreri and Taylor 1996; Fabrizio and others 2001).

A combination of high angler effort and high daily kill limits likely led to high angling mortality of Harrison Lake Bull Trout, and thus low relative population size in the 1970s. Seasonal road access, high levels of non-motorized backcountry travel, high angling license sales and oral history records of high use at nearby sites all are indirectly indicative of substantial angler effort. Road access to fish populations in particular is known to result in high angler effort (Carpenter and others 1994; Newman and Hoff 2000; Cox and Walters 2002) and has been associated with abundance declines in slow-growing, late-maturing charr stocks (Fitch 1997; Gunn and Sein 2000), including several mountain Bull Trout populations (Donald and Stelfox 1997).

Two regulatory measures, each affecting a different sub-population of anglers, and both superimposed on a general decline in angling license sales and backcountry use, likely reduced angling effort and angling mortality of Bull Trout at Harrison Lake after 1988. First, the local access road was permanently closed to vehicle use in 1988, thereby eliminating motor vehicle supported angling opportunities. After 1988, all access to Harrison Lake required a minimum 3-day, 70 km round trip by horse or foot. Second, CR regulations for native trout and charr were imposed in 1994. Although not a direct control on angler effort, their implementation led to a reduction in commercially supported 'trip-angling' effort as outfitters redirected angling effort to other waters. The latter response was not predicted, but supports the views of Cox and Walters (2002) that commercially guided angling effort in remote areas may decline if harvest opportunities for paying clients are curtailed. Recent angler-effort is believed to be less than 5 angler-hr·ha^{-1}·yr^{-1}. Elsewhere, the effects of CR regulations on angling effort have been equivocal, with effort being known to increase, decrease or both after their implementation (Johnson and Carpenter 1994; Muoneke 1994; Newman and Hoff 2000; Sullivan 2003).

Reductions in the biomass and size of *Daphnia* in pelagic waters of Harrison Lake beginning in 1997 support our view that increased Bull Trout abundance occurred after restrictive regulations were imposed, not before. Prey abundance and/or the mean size of individual prey are known to decline in response to increased fish abundance (Reimers 1979; Post and Cucin 1984; Hamrin and Persson 1986; Luecke 1990; Carpenter and others 1987). *Daphnia* decline was coincident with anecdotal observations that large numbers of post-closure Bull Trout appear to have recruited to pelagic waters after 1996 (Wilhelm 1998). Aggregations of 50-150 post-closure Bull Trout were regularly observed in shallow littoral waters in 1995 and 1996, but not afterwards. Interference interactions between large and small Bull Trout (Wilhelm 1998; Wilhelm and others 1999) probably limited post-closure cohort recruitment to pelagic waters between the early 1990s and 1997. Size-based interference interactions are commonly observed in size-structured salmonid populations (Johnson 1976; Tabor and Wurtsbaugh 1991, L'Abee-Lund and others 1993; Damsgård and Ugedal 1997; Post and others 1998, 1999; Biro and others 2003).

The inferred increase in the abundance of Harrison Lake Bull Trout is consistent with increases in Bull Trout spawner abundance reported in the decade following closure of remote Pinto Lake (Herman 1997, ~6-fold) to angling and the implementation of CR and area closures on Lower Kananaskis Lake (Mushens and others 2001, ~20-fold). Clearly, substantial increases in adfluvial or lake-resident Bull Trout abundance may follow elimination of direct angling mortality on exploited waters, provided that populations have not been recruitment overfished. Rapid abundance increases in these adfluvial Bull Trout populations run contrary to observations of decades long recovery histories following exploitation of similarly slow-growing and late-maturing Lake Trout. Density-independent recruitment and survival rates were thought to restrict abundance increases after Lake Trout population sizes were reduced (Walters and others 1980; Mills and others 2002a, 2002b).

Comparing the small differences in climate means between the decades prior to the 1970s and 1990s/2000s to the comparatively large differences in lake accessibility and probable angling effort, changes in climate seem unlikely to be solely responsible for the observed change in Bull Trout growth rates and population size between the periods.

Osprey Lake

In contrast to Harrison Lake, the implementation of increasingly restrictive retention limits in the 1990s, followed by prohibition of angling in 1997, had insignificant impact on Bull Trout abundance in Osprey Lake. Neither mark-recapture population estimates nor mixed-mesh gillnet CPUE provide evidence for an increase in population size between 1980 and 2001. As expected due to the lack of evidence for change in abundance, there was no evidence for changes in Bull Trout length or mass at age between 1979/1980 and 2001/2002. Although high CPUEs from short small-mesh gillnets in Osprey Lake in the 2000s contradict other evidence for lack of abundance change, these likely reflect strong shoreline orientation by Osprey Lake Bull Trout, most of which were captured within 3 m of shore. As a result, short nets necessarily yielded higher CPUEs than long nets, large portions of which fished infrequently occupied offshore waters.

The apparent lack of Bull Trout abundance response at Osprey Lake was surprising considering the high vulnerability of the Bull Trout to anglers (⅓ of the adult trout present were captured with an angler effort of 1 angler-hr ha^{-1} on 19 June 2001, Parker unpublished data), high bag limits and the presence of road access to Osprey Lake for much of the 20th Century. Several possible reasons for the lack of numeric response, none mutually exclusive, seem plausible. First, restrictive regulations may not have substantially reduced angling mortality of Bull Trout after 1990. Due to its proximity to a major tourist highway, Osprey Lake remains heavily visited during the summer months and a small number of visitors have continued to illegally fish the lake. Even a low level of illegal angling, particularly if combined with retention of catch, could be sufficient to preclude increased Bull Trout abundance in small stocks where catchability is high. Low rates of angler non-compliance are thought to mitigate the benefits of restrictive angling regulations (Gigliotti and Taylor 1990; Post and others 2003; Sullivan 2003).

Additionally, perhaps immigration of stream-resident Bull Trout from the unexploited population in the outflow stream provided a recruitment subsidy to Osprey Lake when bag limits were high prior to 1995. If immigration rates were sufficiently high, Bull Trout abundance could have been maintained even if Osprey Lake functioned as a mortality trap. Continuing immigration of Bull Trout from unexploited tributary populations would explain the long-term persistence of Osprey Lake Bull Trout in the face of both heavy angling pressure and the stocking of congenerics, which led to the collapse of much larger adfluvial populations of Bull Trout in larger, but similarly accessible lakes (Donald and Stelfox 1997).

Trophic compensation may also have occurred within the Osprey Lake Bull Trout population, such that any decline in angling mortality of adult Bull Trout has been replaced, at least in part, by inter-cohort cannibalism. Osprey Lake contained at least one giant cannibal (an adult trout large enough to cannibalize other *adults*) in 2001 (696 mm FL, $\delta^{15}N$ 12.25‰ compared to a mean $\delta^{15}N$ of 9.61‰ for all other sampled individuals, Parker unpublished data). Attempted cannibalism of one gillnetted and one angled adult Bull Trout by this individual was directly observed. Inter-cohort cannibalism is a common feature of size-structured Bull Trout (Beauchamp and Van Tassell 2001) and charr populations elsewhere (Johnson 1976; Griffiths 1994; Hammar 2000). If trophic restructuring is common following reductions in angling effort and mortality, a broader definition of population recovery that extends beyond abundance change is required. Such a definition, which might include the recovery of natural ecological interactions within fish populations, may be particularly applicable to watersheds in protected areas, where maintaining unperturbed ecological functions has an equivalent or higher priority than providing legal harvest opportunities to anglers.

Multiple cohort replacement in Harrison Lake

The negative growth rates, low fecundity and eventual demise of at least 15 year-classes of large-bodied pre-closure Bull Trout from Harrison Lake between 1997 and 2001 and contrasting high survival and growth of post-closure Bull Trout was the most interesting feature of Bull Trout population dynamics following the implementation of restrictive angling regulations. Increased exploitive competition and reduced resource density, leading to lower per capita food consumption, as Bull Trout abundance

increased, combined with size-based competitive asymmetries favouring smaller post-closure Bull Trout are proposed to be responsible for the loss of the pre-closure cohorts.

First, large individuals have greater absolute metabolic demands than small individuals and thus greater per capita prey requirements (Claessen and others 2000; Hjelm and Persson 2001). As food resources declined in abundance after post-closure cohorts recruited to pelagic waters, as evidenced by reduced *Daphnia* biomass and chironomid density, pre-closure Bull Trout appear to have been unable to maintain sufficient food consumption to meet their greater metabolic demands, as shown by their low food consumption relative to smaller size classes (see also Chapter Five). Contributing to this failure, post-closure cohorts appear to have truncated the feeding niche of pre-closure Bull Trout by reducing the abundance of the large *Daphnia* (>2.5 mm length) consumed by pre-closure cohorts. The abundance of large *Daphnia* decreased by ~15-fold comparing 1997-2001 to earlier years. *Daphnia* comprised 59% of the stomach contents of large pre-closure Bull Trout in the 1970s (Anderson and Donald 1978) when large *Daphnia* were abundant, but only 1% in the late 1990s. Competitors with exclusive access to a food resource, in this case post-closure Bull Trout, have a competitive advantage over those whose feeding niche includes only shared resources (Schoener 1974).

Second, foraging costs increase with predator:prey size ratio (Kerr 1971; Pazzia and others 2002; Sherwood and others 2002) because single predation events yield a relatively smaller proportion of the maintenance ration as fish size increases. Predator:prey size ratios were greater for pre than post-closure Bull Trout, for all prey types examined, thus pre-closure Bull Trout were energetically inefficient foragers relative to post-closure Bull Trout. We cannot rule out that increased interference competition interactions among individuals as their abundance increased (Boisclair and Leggett 1989) also contributed to the demise of large Bull Trout by increasing their energy expenditures at a time when food resources were depressed.

Competitive asymmetries favouring small-bodied individuals have previously been inferred or documented for both zooplanktivorous (Hamrin and Persson 1986) and omnivorous (Persson and others 2000) fish, including other charr species (Snorrason and others 1991). However, these studies considered competitive asymmetries within the context of providing explanations for cyclic population dynamics, not the effects of changing fisheries management regimes.

Genetically determined aging combined with random physiological wear and tear (Craig 1985) may have contributed to the failure of some pre-closure individuals by further reducing their fitness relative to younger fish. However, it seems unlikely to be responsible for the near simultaneous loss of at least 15 year-classes of large Bull Trout, which in themselves varied in relative age by more than 2-fold and in some cases were little older than the individuals that replaced them. High rates of parasitism in old, large fish have also been implicated in reducing survival rates in large charr (Hammar 2000). However, the role of parasitism, if any, in mediating the loss of pre-closure Bull Trout cannot be assessed because parasite loading was not monitored as part of this study.

CONCLUDING REMARKS

The imposition of restrictive angling regimes had variable effect on the abundance and population structure of two small populations of Bull Trout. Our observations are consistent with variable response in Bull Trout abundance in waters outside the mountain national parks of Canada (Herman 1997; Mushens and others 2001; Doran and others 2003; Paul and others 2003) that were subject to similar regulatory changes. It is probable that abundance increase will not be a consistent feature of increased regulatory protection across all populations of Bull Trout. A variety of factors, including angler non-compliance with regulations and trophic compensation within populations, may limit abundance responses in some waters. Further, some populations may have been recruitment overfished or be subject to depensatory factors (Post and others 2001; Walters and Kitchell 2001) that will preclude abundance increases even if angling mortality is eliminated. Although few studies have considered the role of inter-cohort interactions in fish populations responding to reductions in angling mortality, our work suggests these may be important in determining the response trajectories of size-structured Bull Trout and other fish populations.

This work does not consider the effects of other native or non-native charr species on Bull Trout population recovery following regulatory changes. We note that for Harrison, Pinto and Lower Kananaskis lakes, where large Bull Trout abundance increases occurred following reductions in angling mortality, that no other *Salvelinus* species were present. It is unknown if reductions in angling mortality on Bull Trout would result in increased Bull Trout abundance where non-native *Salvelinus* species have been introduced. Congenerics may compete (Donald and Alger 1993) and hybridize with (Kanda and others 2002) and eventually replace Bull Trout (Donald and Stelfox 1997). Selective removal of non-native Brook Trout by anglers (Paul and others 2003) combined with mandatory CR of Bull Trout failed to permit recovery of Bull Trout in a small Alberta stream. Incidental catch-and-release mortality on the few remaining, but relatively easier to catch, Bull Trout may have played a role in preventing an increase in Bull Trout abundance in this case (Paul and others 2003).

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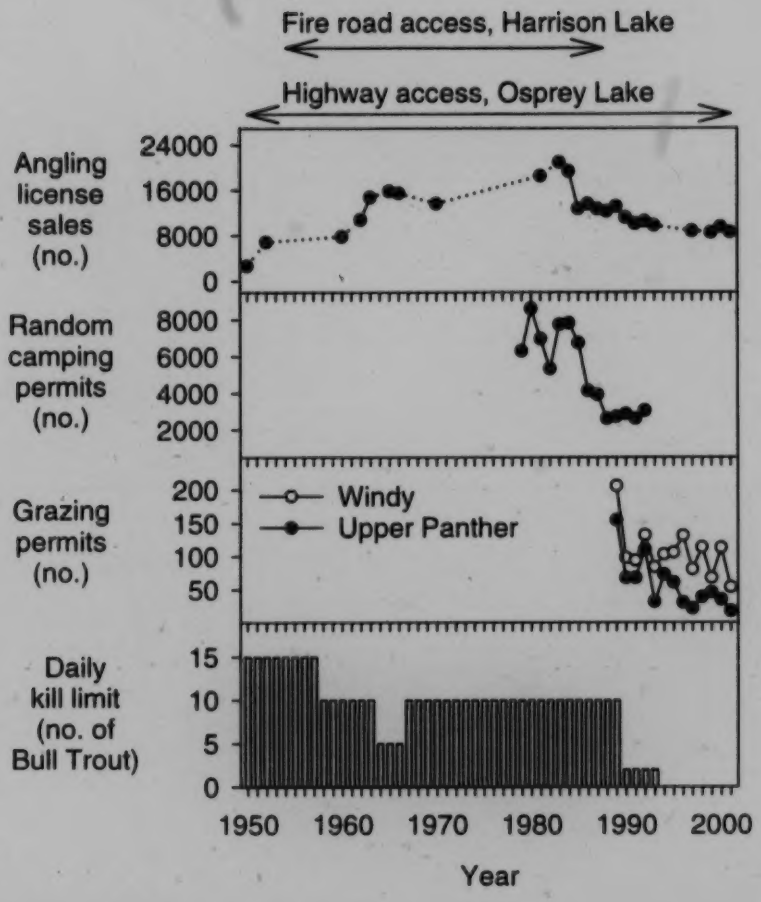

Figure 4.1: Angler-effort indices and Bull Trout retention limits for 1950-2001. Fishing license sales are for the mountain park block (Banff, Jasper, Kootenay, Waterton Lakes and Yoho National Parks combined). Random camping permit sales are specific to Banff National Park. The implementation of catch-and-release angling regulations occurred in 1994 for Banff National Park and in 1995 for Jasper National Park, otherwise kill limits were similar.

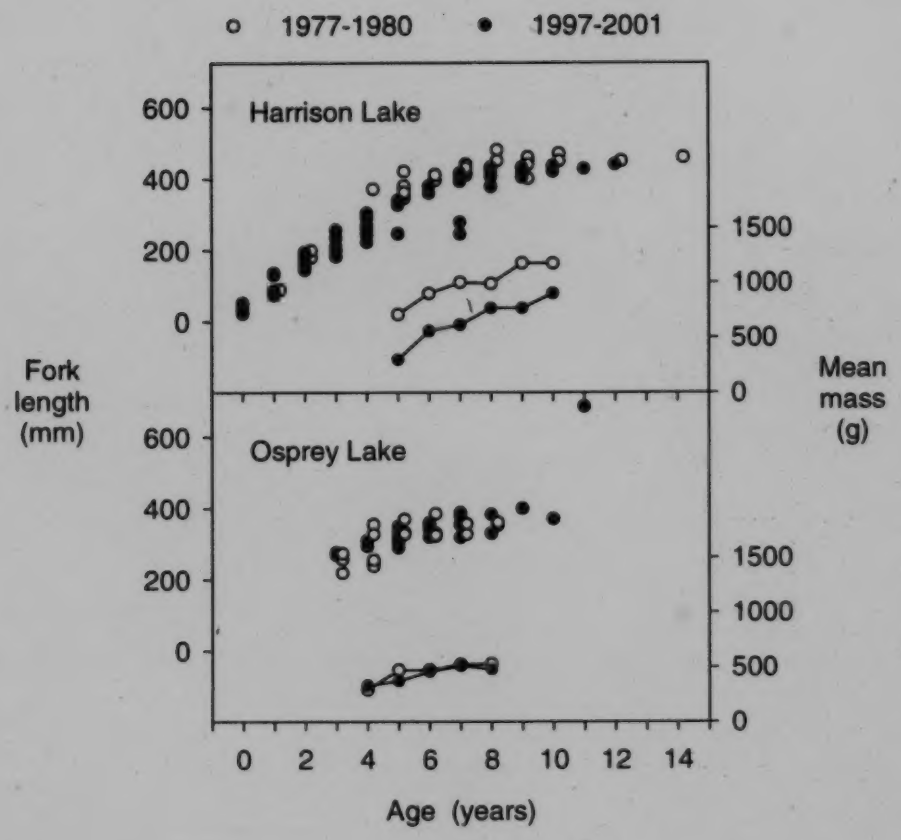

Figure 4.2: Individual fork length and average mass at age for pre-closure and post-closure Bull Trout for Harrison and Osprey lakes.

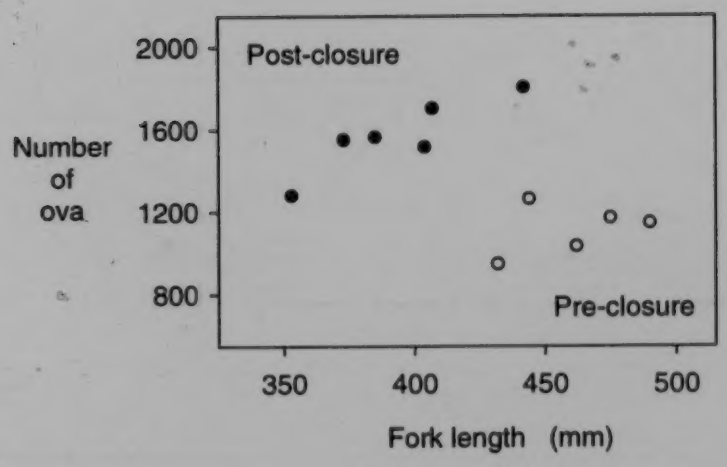

Figure 4.3: Fecundity of Harrison Lake Bull Trout. Post-closure fecundities from Bull Trout captured between 1997 and 2001. Pre-closure fecundities from Bull Trout captured between1997 and 1999.

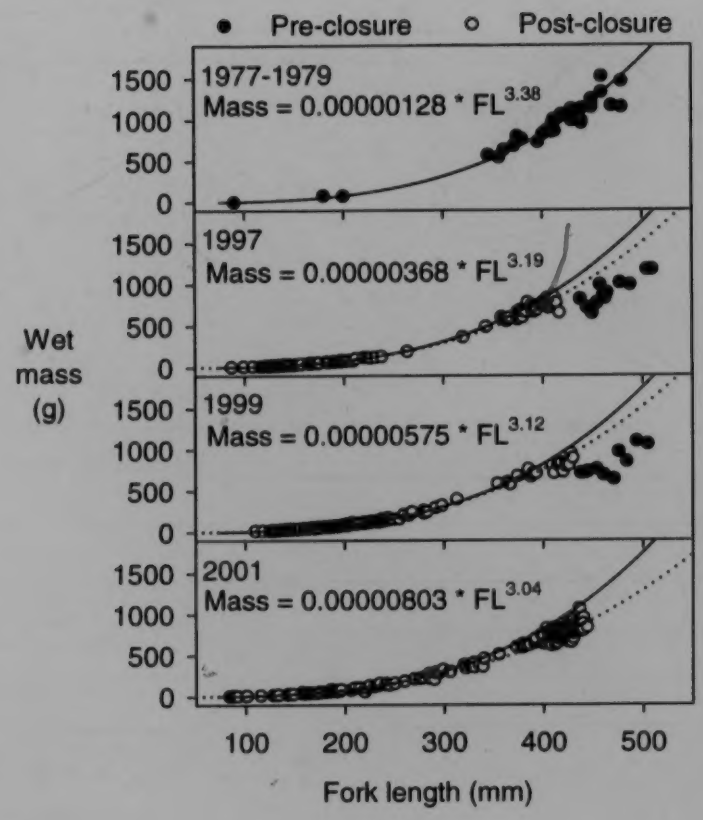

Figure 4.4: Fork length and mass for Harrison Lake Bull Trout of > 75 mm FL. Solid regression line, same on all plots, for 1977 – 1979 pre-closure Bull Trout.

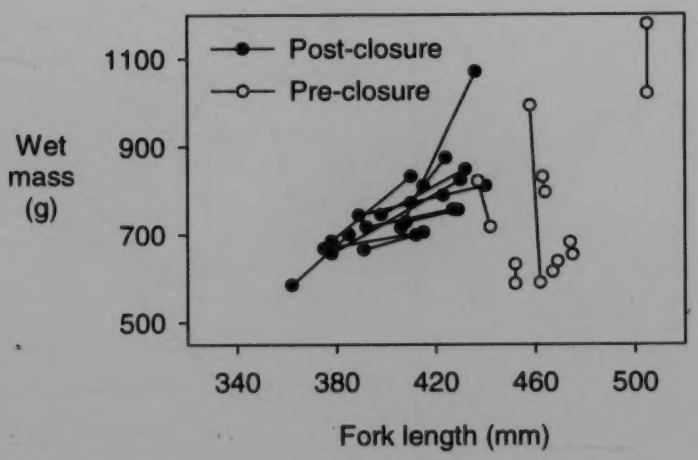

Figure 4.5: Growth trajectories for Harrison Lake Bull Trout marked between 1997 and 1999 and recaptured between 1998 and 2001. Length and mass consistently increase for post-closure Bull Trout. Mass decreases for all pre-closure Bull Trout, while length increases, remains stable or decreases with time.

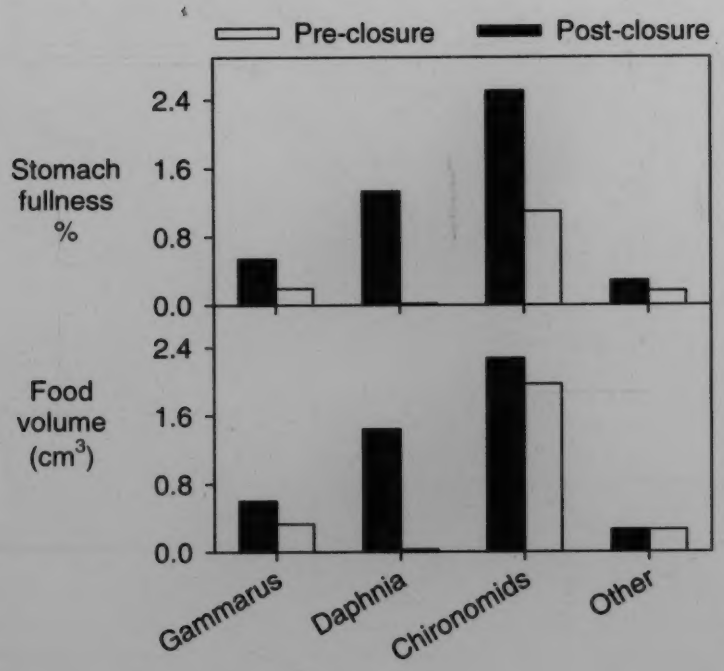

Figure 4.6: Diet composition and mean percent stomach fullness of pre-closure and post-closure Bull Trout between 1997 and 1999.

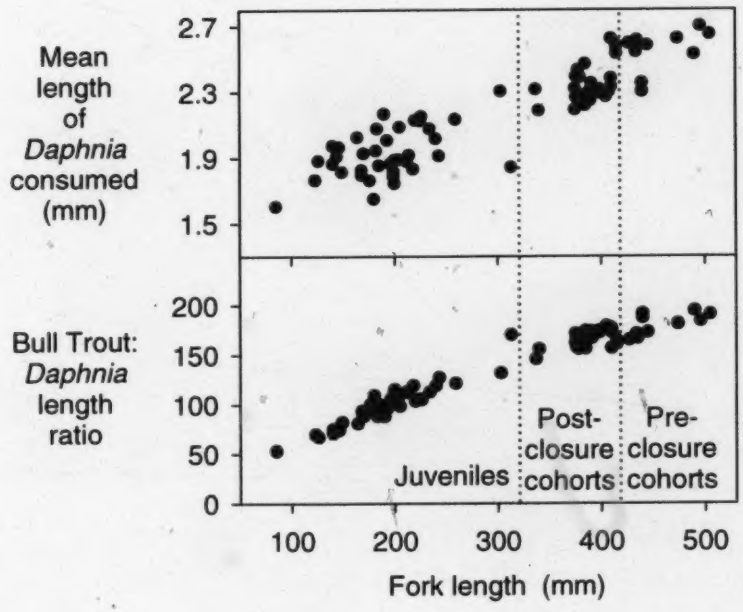

Figure 4.7: Mean length of *Daphnia* consumed by Bull Trout and Bull Trout:*Daphnia* length ratio.

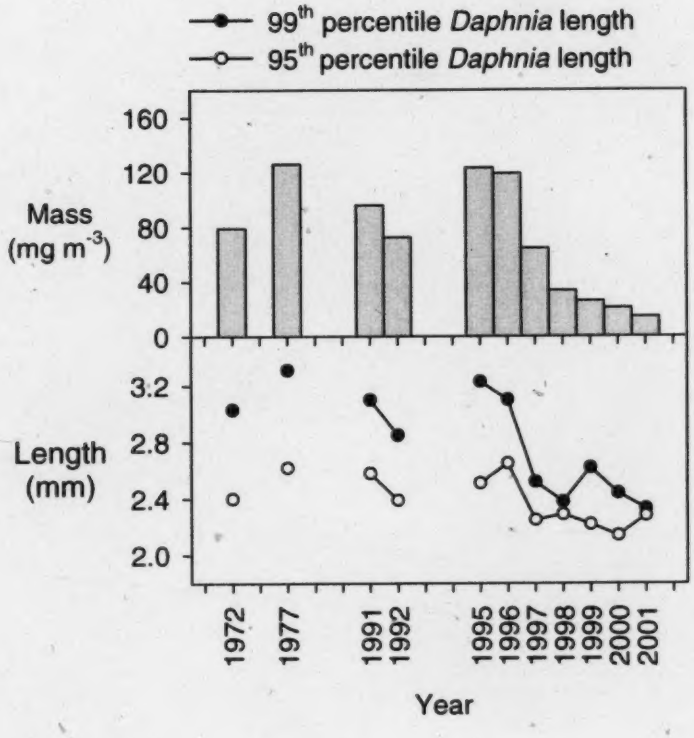

Figure 4.8: August *Daphnia* biomass and 99th and 95th percentile *Daphnia* length for Harrison Lake.

CHAPTER FIVE: BEHAVIOURALLY-MEDIATED CONSEQUENCES OF LOON PREDATION ON A SIZE-STRUCTURED BULL TROUT POPULATION

INTRODUCTION

Predators affect their food resources directly and indirectly through their interactions with the prey community. Direct consumption can be a substantial cause of mortality for both natural (Kennedy and Greer 1988; Rudstam and others 2004) and cultured prey populations (Modde and others 1996; Glahn and others 1999) and may control the size-frequency distributions and abundance of individual prey species (Power 1984; Steinmetz and others 2003). However, the indirect effects of predation, involving the exposure of prey to predators or the presence of predator chemical cues (Nyström and Åbjörnsson 2000), may offset or amplify direct effects. For example, refuge-seeking by prey (Power 1984; Tonn and others 1992; Logerwell and Hargreaves 1996; Layman and Winemiller 2004) can reduce food consumption if prey avoid risky but otherwise profitable habitat (McDonald and others 1992; Post and others 1998) or if prey density and thus exploitive competition increases in food-limited predation refuges (Power 1984). These responses may result in reduced individual growth rates (Werner and others 1983; Fraser and Gilliam 1992; Allouche and Gaudin 2001; Biro and others 2004) reproductive output (Fraser and Gilliam 1992) or prey population growth rate (Nelson and others 2004). Alternately, reduced prey density may lower exploitation competition among surviving prey and permit increased individual growth rates (Van Buskirk and Yurewicz 1998). Prey growth rates may also increase if resource levels increase in response to reduced prey activity (Peacor 2002).

Prey size is an important determinant of the outcome of predator-prey interactions (Werner and Hall 1974; He and Kitchell 1990; Steinmetz and others 2003). However, few studies (Werner and others 1983; Tonn and others 1992) have considered the role of size-based interactions among prey in determining the indirect effects of predation. Where prey are size-structured, size-based interference and/or exploitation interactions among prey often leads to size-based habitat segregation (Post and others 1998). Predator-induced avoidance behaviour by one or more size classes potentially disrupts or enhances this segregation and thus might alter the intensity of interactions among the prey. If cannibalism is an important component of intra-specific interference interactions, as it is in many fish species (Smith and Reay 1991), and prey size varies by several-fold or more, then trophic restructuring of the prey population may be a consequence of changes in interaction intensity. The indirect effects of predation on prey would thus vary asymmetrically with prey size. The trophic restructuring of food webs as an indirect result of predation has been previously reported for both aquatic (Carpenter and others 1987), and terrestrial ecosystems (Schmitz and others 1997), although via different mechanisms.

Here we report the effect of a piscivorous diving bird, the Common Loon (*Gavia immer*) on interactions between juvenile and adult size-classes of normally size-segregated and facultatively cannibalistic Bull Trout (*Salvelinus confluentus*). Based on our preliminary observations of loon-Bull Trout interactions we hypothesized that, in the presence of a loon, predator-avoidance behaviour by adult Bull Trout would result in the loss of size-segregation between pelagic adult and littoral juvenile Bull Trout. We further hypothesized, as a result, that the intensity of interactions between adult and juvenile Bull

Trout, expressed as the rate of cannibalism by adult on juvenile Bull Trout, would increase, leading to partial trophic restructuring of the prey population. Last, we hypothesized that food consumption would increase in adult Bull Trout when a loon was present, due to the cannibalism of juvenile Bull Trout, but fall for juvenile Bull Trout, which were subject to predation by both loons and adult Bull Trout. To test our hypotheses we compared Bull Trout habitat use, and diet, by size class, in the natural presence and absence of a loon in a small alpine lake.

METHODS

Study site

Harrison Lake is an 8.4 ha, 10.7 m deep, alpine lake (2243 m asl) in Banff National Park, Alberta, Canada (51°32'W, 115°48'N). The lake is a sediment-lined bowl surrounded by an ice-scoured shelf of variable width and up to 1 m depth. No submerged or emergent vegetation is present. Harrison Lake is cold (maximum summer surface water temperature 12-16°C between 1991 and 2004), oligotrophic (total phosphorus 3-14 ug L^{-1}) and transparent (Secchi disc depth 5-10.7+ m). The lake contains a population of 400-500 Bull Trout of 100-450 mm fork length (FL) that is recovering following a reduction in angling mortality after 1988 (Chapter Four). Abundance information is not available for smaller Bull Trout. No other fish species occur in Harrison Lake. Most Bull Trout present are at least theoretically vulnerable to loon predation: although smaller fish (10-70 g) are predominant in the diet of loons (McIntyre and Barr 1997), loons may consume fusiform fish at least as large as 410 mm length (Flick 1983).

Because of Harrison Lake's small size, shallow depth, high transparency and lack of structural cover in deep water, it does not offer juvenile and adult Bull Trout a pelagic/profundal (hereafter pelagic) predation refuge from loons. All identified refuge sites, characterized by the presence of overhead cover, occur in littoral habitat < 30 cm deep. These comprise an undercut bank of ~1 m^2 area near the lake outflow, an abandoned and partly collapsed beaver (*Castor canadensis*) bank tunnel of similar area and a group of ~15 woody stems of ~15 cm diameter, derived from subalpine fir (*Abies lasiocarpa*) krummholz. Interstitial spaces among patches of shoreline cobbles comprise refuge habitat for small Bull Trout (< 150 mm FL). In general, in the absence of a loon, small Bull Trout are associated with shoreline cobble, juvenile Bull Trout (150-299 mm FL) with the three described littoral predation refuges and adult Bull Trout (300+ mm FL) with pelagic habitat (Figure 5.1).

Single loons were irregular visitors to Harrison Lake. Between 1996 and 2001, single loons were observed on ~10% of days research staff were present, and only in September. In 2001, loons were present on 7 of 14 days research staff were present, including at least one day during every month of the 4-month ice-free season. We presume one or more loons were locally resident in 2001 and included Harrison Lake among a series of alternate feeding lakes. No loon breeding occurs on Harrison Lake; the nearest known nest site is ~11 km distant.

Bull Trout distribution/abundance

To assess whether the presence of a loon caused a change in habitat use by juvenile and/or adult Bull Trout, we determined: 1) the FL frequency distributions of Bull

Trout in littoral (< 1 m deep) and pelagic habitat (≥ 1 m deep); and, 2) the number of Bull Trout occupying littoral habitat; on three days with (July 11, August 2, August 20) and three days without a loon present (July 12, August 1, August 21), all in 2001. No loon was present on the days immediately preceding each sampling period (July 10, July 31, August 19). Loon presence is defined as the continuous presence of a loon that at least intermittently displayed searching, hunting and feeding behaviour as described by McIntyre and Barr (1997), the latter including surfacing with captured Bull Trout, from approximately sunrise through to the completion of our daily sampling, usually about 13:00 h. Loon absence is the complete absence of a loon on a sampling day.

Based on the results of visual surveys in the 1990s, which identified three commonly used littoral refuges (> 60% of all visible littoral Bull Trout were located within 3 m of one of these sites on any given date, Parker unpublished data), we captured littoral Bull Trout by establishing block nets around known refuge sites, then using dip-nets to capture fish. Netting continued until all visible fish were captured and, in addition, 3 consecutive sweeps with dip-nets under all overhead cover yielded no further individuals. We captured pelagic Bull Trout by a combination of angling, trap-netting and continuously monitored gillnetting with both small (25 and 37 mm stretched mesh, 17-22 m long) and mixed-mesh (25, 37, 50, 75 and 100 mm stretched mesh, 50 m long) monofilament gillnets. Gillnets and trap-nets were set on the bottom, perpendicular to shore, beginning at a minimum depth of 2 m. Sampling of Bull Trout from pelagic and littoral habitats was concurrent. We had earlier sampled littoral refuge habitat on 35 additional days between 1997 and 2001 when no loon was present, we use these data to assess long-term occurrence of adult Bull Trout in littoral waters.

Following capture and the induction of anaesthesia with either methane tricaine sulphonate or clove oil, Bull Trout were measured to the nearest mm FL. Bull Trout were held in continuously flushed lake-water for 30-60 minutes prior to release to permit full recovery from anaesthesia and were released into the same habitat/refuge site from which they were captured. In addition, to permit mark-recapture abundance estimation, the majority of captured Bull Trout of >150 mm FL were marked with a numeric-coded visible implant tag inserted into the adipose tissue behind the eye. Population sizes and associated 95% confidence limits, in parentheses, were obtained from Schnabel multiple mark-recapture population estimation (Krebs 1999) for a subset of juvenile (those of 150-299 mm FL) and, separately, adult Bull Trout.

Reported FL frequency distributions are the mean numbers of captured fish in each FL range for the three days with and without a loon present. To determine if Bull Trout abundance increased in littoral waters in the presence of a loon, we compared the mean number of Bull Trout captured from littoral habitat on days with and without a loon present with a two-sample t-test.

Cannibalism

To determine if the presence of a loon increased the intensity of size-based interactions among the Bull Trout, here operationally defined as the rate of cannibalism by adult on juvenile Bull Trout, we collected 103 Bull Trout stomach content samples on the three above days when a loon was present and 154 on the three days when a loon was absent. We define cannibalism rate to be the proportion of sampled Bull Trout containing

one or more Bull Trout in their stomach contents. Stomach contents samples were obtained by flushing the stomachs of anaesthetized and measured Bull Trout, captured as previously described, using a technique similar to that of Wilhelm and others (2001).

Stomach contents were fixed in 4% formalin and later transferred to 70% ethanol. Stomach contents were sorted and identified using a dissecting microscope. Food items were assigned to one of five categories: Bull Trout, zooplankton (*Daphnia* and *Diacyclops*), chironomids (larvae and pupae combined), macro-benthos (*Gammarus*, larval insects excluding chironomids, oligochaetes and *Pisidium*) and 'terrestrial' (adult Coleoptera, Diptera, Ephemeroptera, Hemiptera, Lepidoptera and Trichoptera). The volume of stomach contents was determined by water displacement following Wilhelm and others (1999). In addition, we measured the FL of all ingested Bull Trout and determined the upper limit of the cannibalism window, here defined as the largest observed ratio of victim FL:cannibal FL. To exclude potential lag effects associated with long digestion times for large juvenile Bull Trout, ie counting a victim cannibalized on a previous day in a current days sampling, we counted only those Bull Trout in stomach contents samples that retained intact skin and scales over the anterior 50% of their body. We excluded 2 instances of cannibalism on this basis.

Binomial confidence limits for cannibalism rates, in parentheses, were calculated following Zar (1999). To determine if a loss of size-segregation resulted in increased cannibalism we compared cannibalism rates, for the days a loon was present, between adult Bull Trout captured from littoral refuge habitat and pelagic waters, using Fischer's exact test (Zar 1999). We similarly tested for differences in cannibalism rate between adult Bull Trout sampled from pelagic habitat on days with and without a loon present.

Stomach fullness

To determine if the presence of a loon affected food consumption in juvenile and adult Bull Trout we tested for differences in % stomach fullness between: 1) juvenile Bull Trout captured from littoral waters in the presence and absence of a loon; 2) adult Bull Trout captured from littoral and pelagic waters in the presence of a loon; and, 3) pelagic adult Bull Trout in the presence and absence of a loon; using the normal approximation to the non-parametric Mann-Whitney U-test (Zar 1999). We determined % stomach fullness for each individual Bull Trout from:

$$\% \text{ fullness} = 100 \times \left(\frac{\text{prey volume cm}^3}{a \times \pi (a/4)^2} \right)$$

where the denominator estimates full stomach volume and a = distance between the origin of the pectoral and pelvic fins in cm. Calculation of % stomach fullness scales stomach contents volume to fish size and permits comparison of relative stomach fullness among size classes. For plotting, % stomach fullness for total food contents and each prey category was averaged over all individuals in each size class, in both the presence and absence of a loon.

To indirectly assess the possible effect of changes in average % stomach fullness on Bull Trout growth rates, we plot similarly determined average % stomach fullness data and daily FL increments calculated for juvenile Bull Trout marked and recaptured in the

summers of 1997, 1999 and 2001. Daily FL increments provided are the simple means for all marked and recaptured juvenile Bull Trout at large for at least 30 days between their first and last capture within each year.

Population level effects

To assess the relative contribution of loon predation and Bull Trout cannibalism to Bull Trout mass loss when a loon was present, we extrapolated sample cannibalism estimates to the Bull Trout population as a whole, using our mark-recapture population estimates. Estimated daily consumption rates by a single loon were taken from McIntyre and Barr (1997). Although we continuously observed individual loons during our sampling, we could not assess the total number of Bull Trout consumed: loons often swallow small prey prior to surfacing (McIntyre and Barr 1997).

RESULTS

Bull Trout distribution/abundance

In the absence of a loon, an average of 37 juvenile Bull Trout were collected from littoral refuge habitat while adult Bull Trout were collected only from pelagic waters (Figure 5.2). In total, 3 juvenile Bull Trout were collected from pelagic waters, although all were entangled within 2 m of the shoreward end of set gillnets. Our littoral catches retained a high proportion of the 51 (38-77) juvenile Bull Trout estimated to be present in August 2001, thus our sampling protocol was efficient with respect to capturing these individuals.

In contrast, in the presence of a loon, all juvenile and an average of 20 of the estimated 352 (200-750) adult Bull Trout were captured from littoral habitat. Because adult Bull Trout were observed to evade encirclement by block nets on several occasions, their abundance in littoral refuge habitat when a loon was present was underestimated. While the number of adult Bull Trout captured from littoral habitat was only 5-10% of their total abundance, their density in individual patches of refuge habitat often exceeded 10 individuals m^{-2}. The abundance of juvenile Bull Trout did not significantly decrease when adult Bull Trout occupied littoral refuge habitat. However, we observed juvenile Bull Trout to increase use of habitat 3-5 cm deep and immediately adjacent to the shoreline when adults were present.

Thus, in the presence of a loon, a portion of the adult Bull Trout occupied littoral predation refuges concurrently with juvenile trout and hypothesis 1 is supported. Refuge seeking by adult Bull Trout in the presence of a loon led to the loss of size-segregation between juvenile and adult Bull Trout.

Cannibalism

In the absence of a loon, chironomids, macro-benthos and *Daphnia* dominated the diet of both juvenile and adult Bull Trout (Figure 5.3) consistent with the earlier observations of Wilhelm and others (1999) for the same population. Both size-classes consumed small (young-of-year [YOY] and yearling) Bull Trout of < 100 mm FL and < 3 g wet mass (Figure 5.4). However, the incidence of cannibalism was low, 0.012 (0.002 - 0.043) and 0.033 (0.011 - 0.076) for juvenile and adult Bull Trout respectively, and, on average, Bull Trout contributed little to the diet of either group (Figure 5.3).

In contrast, in the presence of a loon, the cannibalism rate among adult Bull Trout occupying littoral refuge habitat, 0.354 (0.191 - 0.546), was more than an order of magnitude and significantly ($p < 0.01$) larger than observed in pelagic adults in the absence of a loon. Cannibalism among littoral adult Bull Trout was also significantly greater ($p < 0.01$) than observed for adults in pelagic habitat when a loon was present, 0.085 (0.018 - 0.231). The cannibalism rate for adults in pelagic habitat in the presence of a loon (0.085) was not significantly greater ($p = 0.08$) than that observed in the same group and habitat in the absence of a loon (0.033). We did not observe cannibalism by juvenile Bull Trout in the presence of a loon.

Because cannibalism rate increased in the presence of a loon, hypothesis 2 is supported. Size-based interference interactions among the Bull Trout increased when size-based habitat segregation was lost in the presence of a loon.

Coincident with increased cannibalism, the mean wet mass and FL of Bull Trout consumed by adult Bull Trout increased when a loon was present, to 53 g and 158 mm FL, due to the addition of juvenile Bull Trout to their diet (Figure 5.4). This shift, which reflected the co-occurrence of adult and juvenile Bull Trout in the same refuge habitats, increased the number of cannibalism vulnerable age classes of Bull Trout from two (YOY and yearlings) to at least four (YOY through age 3) when a loon was present.

The upper limit of the cannibalism window was 54% of predator length. Two observed instances of attempted cannibalism of relatively larger prey (> 0.56) resulted in the death of both the cannibal and the victim.

Stomach fullness

In the presence of a loon, % stomach fullness for adult Bull Trout in littoral habitat was significantly greater (Mann-Whitney normal approximation, n_1 and $n_2 = 31$ and 35 respectively, $z = 2.41$, $p < 0.01$) than that of pelagic adult Bull Trout (32.3% versus 7.8%), entirely as a result of the increased contribution of Bull Trout to the diet of the former (Figure 5.3). Although % stomach fullness was 1.6 fold greater for pelagic adults when a loon was present (7.8%) than for pelagic adults when no loon was present (4.9%), again largely due to the increased contribution of juvenile Bull Trout to their diet, there was not a statistically significant difference in median stomach fullness (Mann-Whitney normal approximation, n_1 and $n_2 = 74$ and 35 respectively, $z = 1.17$, $p = 0.12$). In contrast to the case for adult Bull Trout, % stomach fullness was significantly (Mann-Whitney normal approximation, n_1 and $n_2 = 79$ and 37 respectively, $z = 2.85$, $p < 0.01$) lower for juvenile Bull Trout in littoral habitat when a loon was present (3.4%) compared to days when a loon was absent (18.6%).

Thus hypothesis 3 is supported. Stomach fullness increased for adult Bull Trout and decreased for juvenile Bull Trout in the presence of a loon.

For the years 1997-1999 and 2001, mean daily FL increments in juvenile Bull Trout were positively correlated with mean % stomach fullness (Figure 5.5).

Population level effects

Estimated population sizes for juvenile and adult Bull Trout were 51 (38 – 77) (~5.7 kg standing mass) and 352 (200 - 750) respectively, in 2001. Assuming 25 of the 352 adult Bull Trout occupied littoral predation refuges when a loon was present,

population-wide daily cannibalism likely increased from ~12 small Bull Trout of < 100 mm FL (< 25 g of Bull Trout day^{-1}) in the absence of a loon, to ~23 small and juvenile Bull Trout, of up to 246 mm FL (~900 g of Bull Trout day^{-1}) when a loon was present. Less than 25 g of the latter total was attributable to small Bull Trout. Considering only juvenile Bull Trout, the mass loss due to loon-induced cannibalism was equivalent to ~16% of standing juvenile Bull Trout mass day^{-1} in August 2001. Numeric losses of juvenile Bull Trout due to loon-induced cannibalism were 15 – 29% of juvenile abundance day^{-1} in August 2001.

DISCUSSION

In the absence of a pelagic avian predator juvenile Bull Trout occupied littoral waters while adult Bull Trout predominantly occurred in pelagic habitat in agreement with Wilhelm and others' (1999) earlier observations for the same population. Similar size-based habitat segregation is common in omnivorous, facultatively cannibalistic fishes (Foster and others 1988; L'Abée-Lund and others 1993; Persson and others1996; Post and others 1998; Biro and others 2003) and is thought to reduce interference competition interactions, including cannibalism, between small and large size-classes.

The induction of an anti-predator behavioural response in adult Bull Trout following the appearance of a loon, which led to their use of littoral refuge habitats, was consistent with strong avoidance of predators previously reported or inferred in numerous field studies. Prey of vulnerable size classes, whether small or large, typically either select low risk, often structurally complex littoral habitats (Savino and Stein 1982; Werner and others 1983; Power and others 1985; Tabor and Wurtzbaugh 1991; Diehl and Eklöv 1995; Crowder and others 1997; Allouche and Gaudin 2001; Biro and others 2004) or emigrate from predator-occupied sites altogether (He and Kitchell 1990; Fraser and Gilliam 1992) following the introduction of predators. However, size-based habitat segregation was lost in Harrison Lake Bull Trout, unlike most reported experimental or natural prey populations where size-based habitat segregation was induced by the addition of predators.

Co-occurrence of juvenile and adult Bull Trout in refuge habitat in the presence of a loon intensified size-based interference interactions between the size-classes. The daily numeric losses of small and juvenile Bull Trout combined, due to increased cannibalism alone, approximately doubled on a daily basis, while biomass losses increased more than 30-fold. The relative numeric losses attributable to loons and Bull Trout combined cannot be assessed, because we could not measure Bull Trout consumption by loons. However, daily biomass losses due to direct loon predation and Bull Trout cannibalism probably were similar based on published estimates of average daily fish consumption by loons (~900 g per day, McIntyre and Barr 1997).

More important than absolute numeric or biomass losses, the number of year-classes of Bull Trout vulnerable to intra-specific predation increased from two to four when juvenile Bull Trout were added to the diet of adults. The induction of cannibalism of older cohorts, which were comprised of small numbers of individuals, should have comparatively greater effect on prey population dynamics than if a similar number of individuals from numerically stronger YOY and yearling cohorts were cannibalized. The low numeric strength of the older cohorts renders them more susceptible to complete

elimination. The estimated daily numeric losses of juvenile Bull Trout to cannibalism equaled 15-29% of estimated juvenile abundance day^{-1} in August 2001. Infrequent visits by loons may thus have biologically significant indirect impacts on the population dynamics of this and other similar small prey populations. Small changes in loon visitation rates through time, on the order of as few as 2-3 days year^{-1}, also would have dramatic impacts on small prey populations.

The described size-based interaction modification also resulted in indirect predation effects on food consumption that were strongly asymmetric across prey size-classes as similarly noted by Werner and others (1983), Tonn and others (1992) and Winkelman and Aho (1993) for other fish species. Strong feeding suppression in juvenile Bull Trout, which were under predation threat by both loons and adult Bull Trout when a loon was present was expected. Activity and feeding suppression is a common behavioural response to increased predation risk (Angradi 1992; Fraser and Gilliam 1992; L'Abée-Lund and others 1993).

Our sampling regimen did not permit direct evaluation of juvenile growth responses to reduction in food consumption. However, because seasonal % stomach fullness was positively correlated with average daily FL increments of juvenile trout, we infer that extended loon presence and associated feeding suppression could limit growth rates of juvenile trout in the long term. Low growth rates may result in juveniles spending increasing periods of time within the predation window of both loons and large Bull Trout and increase their exposure to predation and cannibalism as noted by Werner and others (1983). This may further lengthen the vulnerability window of juvenile Bull Trout beyond that expected from the addition of juveniles to adult Bull Trout diet alone and further increase the risk of year-class elimination.

Although habitat shifts by vulnerable prey generally are associated with reduced food intake (Werner and others 1983; Skelly and Werner 1990; Fraser and Gilliam 1992; McDonald and others 1992; Tonn and others 1992), adult Bull Trout food consumption increased when shifting habitat to avoid predation. This reflects in part the increased cannibalism rate, but more so the large increase in the average biomass of individual prey items consumed. Increased food consumption has rarely been observed in predation-vulnerable prey size-classes exhibiting behavioural responses to predation (but see Peacor 2002). Rather, invulnerable size classes that are able to co-exist with predators are thought most likely to experience growth and/or fecundity benefits as exploitation competition between vulnerable and invulnerable size-classes is reduced (Werner and others 1983; Tonn and others 1992).

Given the observed short-term foraging gain for adult Bull Trout in shallow water, we question why they do not routinely occupy littoral refuge habitat when loons are absent. Optimal foraging theory would predict that utilization of shallow littoral refuge habitats should be preferred, because risk of predation would be low at the same time as food consumption increased (ie the μ/f rule of Gilliam and Fraser [1987] would be minimized). However, not including the work described herein, only a single adult Bull Trout has been collected from littoral refuge habitat in Harrison Lake on 35 additional 'loon-free' sampling days between 1996 and 2001 (Parker unpublished data). Biro and others (2003) similarly reported little use of waters < 1.5 m deep by stocked adult rainbow trout even when juveniles, which were similarly subject to cannibalism, were

abundant in this habitat. Attempted predation of YOY, yearlings and juveniles by adult Bull Trout, with attacks originating from and finishing in deep water were observed (Wilhelm 1998), however such attacks generally included only a few seconds use of shallow water and were not observed to include pursuit into refuge habitat.

Both biological and physical factors may impart costs to extended adult Bull Trout use of shallow littoral waters and preclude their routine residence in littoral refuge habitat. First, predation risk from alternate terrestrial or avian predators may be high. In particular, one or two Bald Eagle (*Haliaeetus leucocephalus*), probable plunge hunters of adult Bull Trout in littoral habitat, were present for part or all of 23 of 41 days sampling crews visited Harrison Lake between 1996 and 2001. As the most frequently occurring predator of adult Bull Trout, this species likely imparts substantial risk to the use of shallow littoral habitat. Eagles and loons did not co-occur on Harrison Lake during the course of this work, thus we were unable to define Bull Trout behavioural responses when both were present. Second, high UV-B exposure, due to a combination of high elevation, low concentration of photo-protective dissolved organic carbon in lake water (< 1 mg L^{-1}) and the shallowness of littoral refuge habitat may impose high physiological costs to littoral residence. Experimental UV-B exposure, at environmentally realistic levels, inflicted surface tissue damage to several high-elevation salmonid species (Little and Fabacher 1994). Last, shallow littoral habitat often was 4-6°C warmer than the deeper and colder (7 - 10°C) pelagic strata generally occupied by adults. The latter temperatures were similar to laboratory determined thermal preferenda for Bull Trout (Selong and others 2001). Adult Bull Trout may preferentially avoid littoral habitat to minimize increased energy expenditures associated with residence in warm water. The body temperature of Bull Trout of 100 -1000 g, which would include most pelagic adults, should equilibrate to the surrounding water within 15 - 30 minutes (Peters 1983), thus comparatively short residence in littoral habitat would result in increased body temperature.

This study considered only short-term behavioural effects occurring on the scale of a few hours following the initiation of loon presence. We speculate that the long-term effects of periodic cannibalism on the fitness of individual adult Bull Trout varies from beneficial to detrimental depending on its frequency. Many salmonid populations in similar small high-elevation ecosystems are small particulate feeders of zooplankton and benthos. Large prey often are absent and stunting is common (Reimers 1979; Donald and Alger 1986; Donald and Alger 1989; Hofer and Medgysey 1997). If infrequent cannibalism permits small increments in the FL of individual trout, then their foraging costs are expected to increase when they return to a diet dominated by small food items because the energetic costs associated with feeding on small particles increase rapidly with fish size (Pazzia and others 2002; Sherwood and others 2002). This may be sufficient to initiate the long-term decline of some large individuals as size-based consumptive asymmetries favouring small body size (Chapter 3; Hamrin and Persson 1986) renders them increasingly competitively inferior to smaller con-specifics.

Alternately, increased cannibalism and thus food consumption, if maintained by a period of high loon visitation, potentially eliminates the trophic bottleneck (Heath and Roff 1996) between invertebrate predation and piscivory that is thought to limit individual size in Harrison Lake Bull Trout (Wilhelm and others 1999) and other

omnivorous fish populations (Diana 1987; Ridgway and Chapleau 1994; Pazzia and others 2002). Because the upper limit to the cannibalism window for Bull Trout is large, ~0.55 of predator body length, as similarly observed by Beauchamp and Van Tassel (2001), modest 50 – 100 mm increments in the FL of the largest adult Bull Trout, as a result of cannibalism of juvenile trout, could allow these individuals access to small pelagic adults and induce the development of giant cannibals (Claessen and others 2002). Bull Trout and other omnivorous salmonids are known to attain 800 mm FL or more when fish, either of the same or another species, are an important item in the diet (Beauchamp and Van Tassell 2001, Fraley and Sheppard 1989).

Observed increases in loon visitation rate at Harrison Lake over the past decade, perhaps as a result of recent increases in Bull Trout population size following reduction in angling mortality (Chapter Three) or the loss of alternate feeding lakes as non-reproducing fish populations collapse following cessation of fish stocking activities in nearby lakes (Schindler and Parker 2002), thus potentially have significant long term impacts on Bull Trout population structure and dynamics.

CONCLUDING REMARKS

In conclusion, we find infrequent visits by single mobile predators may elicit complex and biologically significant indirect population-level consequences for size-structured prey populations. Further, we extend the known range of indirect effects of predation to the include intensification of interference interactions, in this case cannibalism, among size-classes of prey. These indirect effects may both affect prey recruitment and restructure trophic interactions within prey populations. The evaluation of direct predation effects alone is thus insufficient to assess the role of mobile predators on their prey.

Further, we infer that small open ecosystems may be highly sensitive to small changes in the visitation rate of even a single mobile predator. We expect, in anticipation of predicted climate change and expected shifts in the distribution of many species, that new predators will arrive at previously unoccupied ecosystems and that the frequency of occurrence of existing predators will change. Fractional changes in average biodiversity brought about by fluctuating climate or perhaps variation in food resources at adjacent or distant feeding sites, potentially have profound behaviourally-mediated impacts on the receiving ecosystems.

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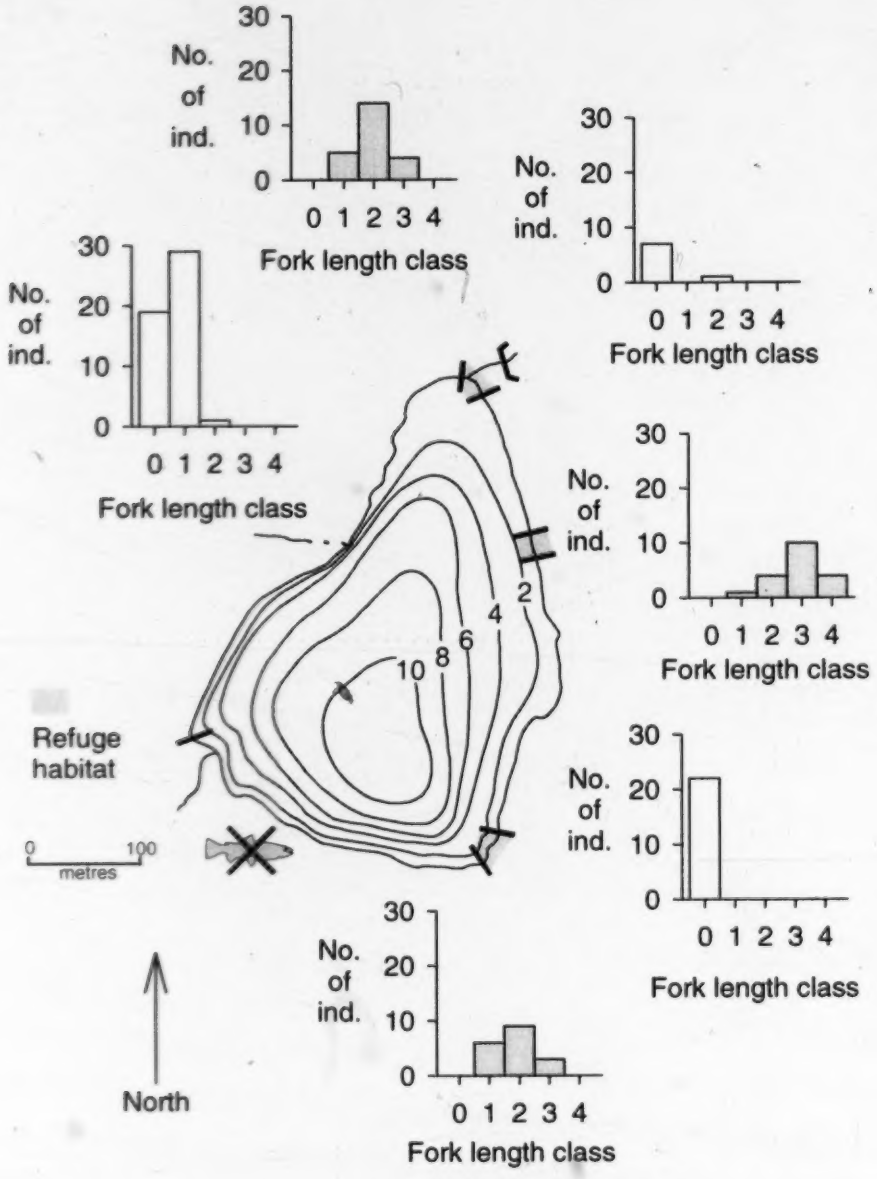

Figure 5.1: Distribution of small and juvenile Harrison Lake Bull Trout in the absence of a loon, as determined by visual shoreline survey. Fork length classes: 0 = 20–49 mm, 1 = 50-99 mm, 2 = 100-149 mm, 3 = 150-249 mm, 4 = 250-300 mm FL. Shaded bars = size distribution in refuge habitats. White bars = size distribution in intervening non-refuge habitats. No trout were observed along the south shore. Depth contours in m.

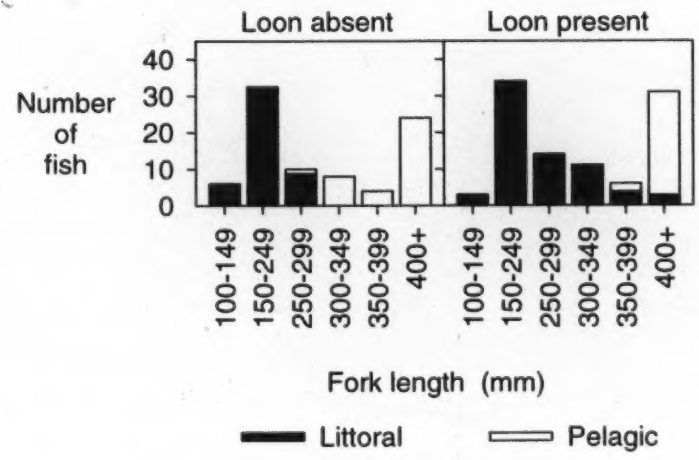

Figure 5.2: Mean FL distributions of Bull Trout captured from littoral and pelagic waters of Harrison Lake in the presence and absence of a loon.

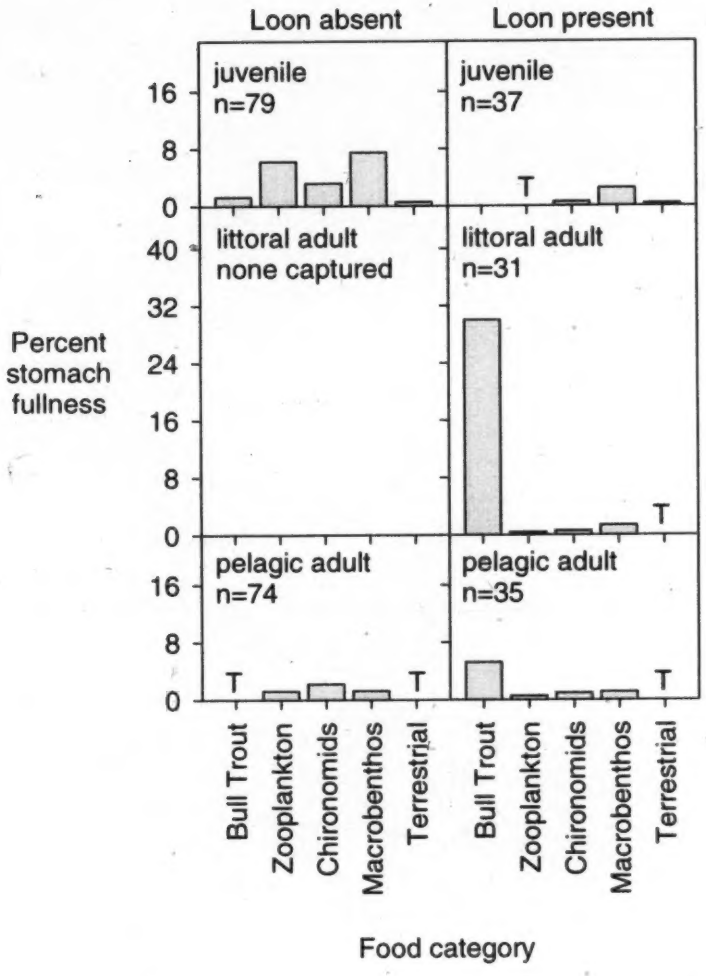

Figure 5.3: Average % stomach fullness, by prey category, and Bull Trout size class, in the absence and presence of a loon. T = < 0.1%.

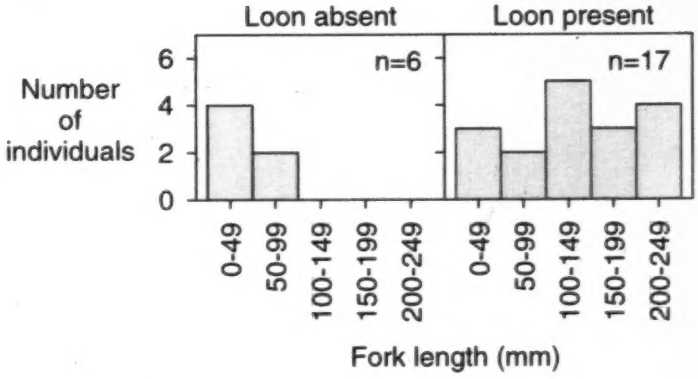

Figure 5.4: Fork length distributions of Bull Trout flushed from Bull Trout stomachs in the absence and presence of a loon.

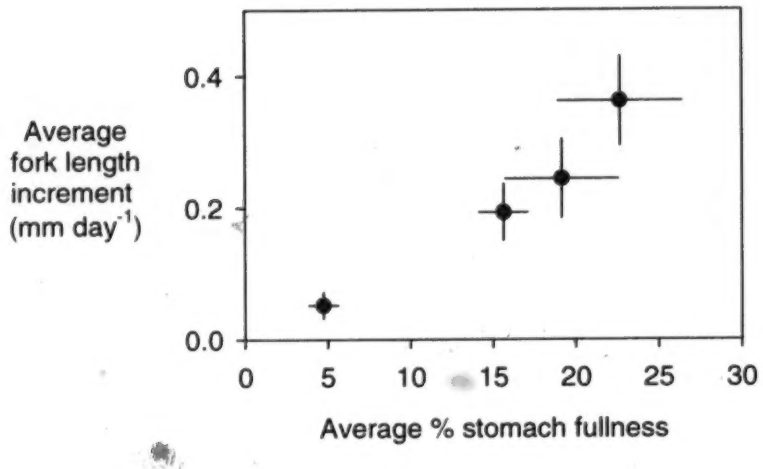

Figure 5.5: Annual mean % stomach fullness and mean daily FL increments for juvenile Bull Trout in the 1990s and 2001. Error bars = 1 standard error.

CHAPTER SIX: GENERAL CONCLUSION

CONCLUDING REMARKS

The partial removal of human influence from the landscape, via the elimination of a non-native fish stock and the near elimination of angling mortality of native fish species, initiated the partial restoration of native invertebrate and fish communities of several high-elevation lakes. Our observations were consistent with the results reported by Herman (1997), Donald and others (2001, and Mushens and others (2001) for montane and subalpine lakes and McNaught and others (1999), Knapp and others (2001) and Schindler and Parker (2002) for high-elevation alpine lakes. In all cases, partial or complete removal of human influences led to at least partial recovery of aquatic communities or abundance increases in formerly exploited fish stocks.

For Bighorn and Harrison lakes, the response trajectories appear to be long, in common with other high-elevation (Anderson 1972; Herman 1997; McNaught and others 1999; Drake and Naiman 2000; Schindler and Parker 2002), montane (Donald and others 2001; Mushens and others 2001), boreal (Schindler 1998; Wissel and Benndorf 1998; Vinebrooke and others 2003) and temperate (Mittelbach and others 1995) lakes. Long-term post-manipulation study is essential to accurately assessing the fate of the communities of these and other manipulated ecosystems. For example, three years of post-manipulation study of Bighorn Lake led to incorrect inferences concerning the probable abundance of phytoplankton relative to those made six years after manipulation began. Because further biotic responses remain possible in future decades, via the invasion of extirpated plankton species, further ecosystem response is likely. For Harrison Lake, where Bull Trout life span approaches three decades and mobile non-human fish predators are adjusting to region-wide losses of numerous alternate feeding lakes and changes in prey abundance in native fish lakes, Bull Trout population size, structure and dynamics may similarly require a long period to stabilize (whether to stationary or cyclic population dynamics). The collection of long-term data is required for evaluating changes in management regimes such as those implemented in the mountain national parks of Canada and the USA.

In contrast to montane and subalpine ecosystems (Donald and others 2001; Knapp and others 2001), ecosystem resilience in high-elevation lakes appears to decrease as the duration of perturbation of high-elevation ecosystems increases (Parker and others 1996; Knapp and others 2001; Schindler and Parker 2002; Sarnelle and Knapp 2004). The degradation of diapausing egg banks, particularly for keystone species such as *Hesperodiaptomus*, imposes finite limits on the resilience of high-elevation invertebrate communities. Unlike lower elevations, where dispersal is less restricted due to high connectedness of watersheds and lower elevation barriers, dispersal limitation in alpine habitats (Sarnelle and Knapp 2004; Holzapfel 2005) constrains the recovery of these ecosystems when perturbations are removed. It is becoming increasingly unlikely that the pristine invertebrate communities of high-elevation lakes stocked with non-native fish prior to 1970, and that currently contain reproducing non-native fish populations, will be successfully restored using fish removal alone. The widespread reintroduction of extirpated invertebrates into alpine waters may be required to complete restoration of these ecosystems. Similarly, the ongoing spread of non-native fishes into waters

previously occupied only by native species (Adams and others 2001; Fredenberg 2002; Paul and others 2003) and hybridization between native and non-native species (Kanda and others 2002) will continue to degrade prospects for the restoration of native fish populations over time.

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APPENDIX 1: POST-SAMPLING CHLOROPHYLL-*a* DEGRADATION

INTRODUCTION

Study lakes were sampled using a combination of foot and helicopter supported access between 1991 and 2002. Due to fixed crew rotation dates when foot-sampling, biological samples were held for 1 - 3 days prior to their delivery to the University of Alberta Limnology Laboratory (UALL). Samples were held, submerged and sealed from water, in a groundwater fed creek, in the dark, at temperatures of = 6°C. In contrast, when conducting helicopter-based sampling, samples were held on ice and delivered to UALL within 10 hours of collection. Differences in access method, and thus storage regimes for biological samples, potentially result in systematic biases in analytical results due to decomposition or growth processes. Because helicopter sampling increased in frequency with time, if systematic bias was present due to differences in sample storage, this bias could confound the interpretation of long-term ecosystem experiments. To determine if differences in storage regimes were likely to confound the interpretation of chl-*a* data, we experimentally tested whether the length of storage of chl-*a* samples had a significant effect on measured chl-*a* concentration.

METHODS

We tested for chl-*a* degradation during cold storage for chl-*a* samples collected, by helicopter, from Bighorn and Pipit lakes on 12 July 2004. For each lake a 40 L sample of epilimnetic lake water was collected using a 275 cm long clear plastic tube. Samples were immediately transported to UALL, arriving within 6 hours of collection. At UALL 20 – 2 L subsamples were filtered through 47 mm GF/F filters to obtain 20 replicate chl-*a* samples. Chl-*a* samples were randomly assigned to one of 5 storage treatments (4 samples each): 0 h, 24 h, 52 h, 75 h and 95 h. Each batch was separately wrapped in aluminium foil to exclude light. 0 h samples were immediately frozen. The remaining samples were sealed from water, double-wrapped in plastic bags, submerged in a water-filled bucket and held in a controlled environment chamber, in the dark, at 5°C for their respective storage periods. Wrapping, underwater storage and storage temperature were similar to that in the field.

On termination of each time period, one batch of filters was removed from the bucket and immediately frozen. At the end of the experiment, all samples were thawed and chl-*a* was extracted using the procedure of Welschmeyer (1994). Chl-*a* was measured using a fluorometer.

We tested for differences in chl-*a* concentration among treatments using one-way ANOVA (Kleinbaum and Kupper 1978). If ANOVAs were significant, we used Tukey's test (Kleinbaum and Kupper 1978) to determine which treatment pairs were significantly different. Differences in treatment means were considered significant to experimental interpretation only if they were both significantly different from the 0 h mean and varied from the 0 h mean by > 10%.

RESULTS AND DISCUSSION

Treatment means and standard deviations are provided in Table A1.1. No significant differences in ch-*a* concentration were detected among treatments for the Pipit

Lake data ($p = 0.81$). Significant among treatment differences were observed for Bighorn Lake ($p = 0.002$) (Table A1.1). Chl-*a* was significantly higher than the 0 h mean at 52 h and lower at 95 h. However, all treatment means varied from the 0 h mean by < 6%.

We conclude that chl-*a* degradation/enhancement either does not occur during short-term sample storage or, if it occurs, is trivial to the interpretation of our experimental results.

REFERENCES

Kleinbaum DG, Kupper LL. 1978. Applied regression analysis and other multi-variable methods. Duxbury Press. North Scituate, Massachusetts.

Welschmeyer NA. 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. Limnol Oceanogr 39:1985-1992.

Table A1.1: Treatment mean chl-*a* concentrations and standard deviations. Lower case letters denote means that are not significantly different. Storage time in h, chl-*a* in mg m^{-3}.

Bighorn Lake				Pipit Lake			
Storage time	Mean	Standard deviation		Storage time	Mean	Standard deviation	
0	0.59	0.02	a	0	0.27	0.09	a
24	0.61	0.02	ab	24	0.29	0.10	a
52	0.63	0.01	b	52	0.31	0.10	a
75	0.60	0.02	a	75	0.32	0.10	a
95	0.56	0.02	c	95	0.34	0.09	a